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ESSAYS UPON HEREDITY

AND KINDRED

BIOLOGICAL PROBLEMS

BY

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VOLUME II

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AUTHOR'S PREFACE TO SECOND VOLUME

The four essays which constitute this Second Volume supplement those of the First, by bringing forward new facts to support the earlier ideas, and by improving and completing the latter on the basis of the most recent discoveries.

The first two essays afford further support to the arguments in favour of the non-transmission of acquired characters, inasmuch as they attempt to prove that these arguments hold in certain cases which at first sight appear to refute them. The diminution of parts which are no longer used has been explained in an earlier essay as the result of the cessation of natural selection, i. e. of panmixia. The conception that every part of the organism is maintained at the level it has reached only by means of the continued activity of natural selection, and that any intermission of this activity leads to a gradual diminution, has passed through many minds. Darwin himself appears to have held this idea, and Romanes, and especially Seidlitz, have more or less clearly expressed it. But the thought first attained its full significance when we arrived at the definite conclusion that the Lamarckian principle of modification had no real existence, because acquired characters, and hence the decrease which organs suffer by disuse, are not inherited. Thus every explanation of the existence of disused parts in a rudimentary state fails, except panmixia; and the conclusion was unavoidable that the countless characters which enter into our conception of a species can only be maintained at their present level by the ceaseless activity of natural selection.

The Second Essay is concerned with the problem as to the origin of those higher mental powers of civilized races which have played no part in the struggle for existence, and the high cultivation of which has been entirely independent of natural selection. I have chosen the art of music as an example, because it presents so deceptive an appearance of improvement by the inheritance of the results of practice from one generation to another.

The Third Essay is an answer to the numerous objections which Prof. Vines of Oxford has advanced against many of my views. The reader of the First Volume will perhaps welcome it, as it elucidates some points upon which I have been frequently misunderstood.

The Fourth and last Essay is not only the longest, but the one to which I attach the chief importance, because my views as to the essential meaning of so-called sexual reproduction, and the allied process of conjugation in unicellular organisms reach their final form in it, having been reconstructed on the basis of various new discoveries. I believe that I have solved, at any rate as regards the main points, the problem of the enigmatical double extrusion of polar bodies from the animal egg, and have explained why only a single division of the nuclear substance does not take place. I hope, furthermore, that I have thus confirmed my views upon the general significance of so-called sexual reproduction,—as a means for producing hereditary individual variations, and for arranging these variations in ever fresh combinations.

My hypotheses have been at times severely handled when shown to be incorrect by the discovery of new facts,—even when these latter were themselves founded on my views. I freely admit that I have made many mistakes;—my explanation of the formation of polar bodies by the egg was at first wrong, then only partially right, and claims to be correct only in the concluding essay. Let who will reproach me: I am not ashamed of this error; on the contrary, I regard it with a certain satisfaction, for I believe it pointed the path to truth. I

have left it unchanged in the essays of the First Volume, not only for this reason, but chiefly because it is, I think, of great interest to trace the development of a scientific truth. Hypotheses, even when not absolutely right, may be of value in advancing our knowledge, if only they are relatively right, i.e. when they correspond with the state of existing knowledge. They are like the feelers which the short-sighted snail stretches forth on its darkened path, testing this way and that, and withdrawing them and altering its route as soon as they come across any obstacle; just as an unyielding fact may show that we are on a wrong road.

Rome was not built in a day, and no scientific truth is at once revealed without a prolonged previous history made up of mingled truth and error. The last word has not yet been spoken on the subject dealt with in these essays; but if we remember the complete obscurity which, only ten years ago, surrounded everything which is now clearly revealed in the final essay, we shall not be able to refrain from an inward feeling of satisfaction. Of course, much remains to be done in this department of biology; but a firm foundation has been laid on which much may be erected.

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Retrogressive Development in Nature.

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A lecture delivered at the 'Akademische Gesellschaft,'
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IX.

RETROGRESSIVE DEVELOPMENT IN NATURE.

Evolution in the animal and vegetable kingdoms is generally understood to mean an uninterrupted progress from lower to higher forms of life. Such a view is not, however, strictly correct; for retrogression plays an important part in evolution, as is shown by the fact that an investigation into the history of degenerate forms often teaches us more of the causes of change in organic nature than can be learnt by the study of progressive ones. Such investigation is, therefore, of the deepest interest.

To begin with a well-known instance, we are all aware of the existence of birds which cannot fly, and of some among them which do not even possess wings. One of these is the Apteryx of New Zealand, called by the natives 'Kiwi-kiwi.' The most superficial observer would at once remark that this bird lacks something, since it reminds one of a man without arms; for the wings are totally absent, and the place where they should be, is covered with a close smooth growth of hair-like feathers.

Not very long ago the question why this bird should lack wings would have been regarded as sufficiently answered by reference to its mode of life. The Kiwi lives in woods, not in the trees, but on the ground; in the day-time it hides in holes in the ground, and comes out warily at night to hunt the worms and insects which form its prey. It has no need of wings to obtain its food, nor does it stand in any fear of native enemies on the ground; for two species of bat are the only representa-

tives of the Mammalia in New Zealand. In former days it would have been said that the Kiwi was created without wings, because it had no need for them ; but now that we can no longer hold the old simple doctrine of special creation, and are compelled to believe that the animals and plants of every age have not been suddenly created out of nothing, but have been developed from ancestral forms, such an assumption can have but little weight. The idea of such special creation is not compatible with the present state of our knowledge; we cannot suppose that the cause of all being called the forms of life into existence in their present form by word alone, but rather by the action of natural forces upon matter, these working together to produce the whole universe of everlasting change, seen in the rise and decline of solar systems, no less than in the evolution and extinction of species. We do not hold that the Kiwi was created out of nothing, but that it was developed from older forms, from species of birds very unlike itself. These birds again were evolved from lizard-like reptiles, which possessed fore- as well as hind-limbs : hence the primitive birds must have had these also, and their fore-legs must have been gradually changed into wings. It is, therefore, certain that the ancestors of the Kiwi possessed wings. Why, then, should the Kiwi have lost them?

Furthermore we have positive evidence in support of the above conclusion that the ancestral form possessed wings, which have been eliminated in the existing species—because the Kiwi even now bears traces of them as minute rudiments hidden under its feathers, and although these no longer serve any purpose, the essential structure of the wing is plainly recognizable, and there are even some short crooked feathers which, with their strong shafts, are very like true primary quills.

The actual reason why the Kiwi possesses only rudimentary wings is, of course, to be found in the fact that, with its present structure and habits, they would be useless to it, and so far we should be justified in saying that the bird has no wings because it has no use for them. The Kiwi is certainly formed for terrestrial life; its short but strong legs and feet are adapted for scratching the earth or digging out holes under the roots of great trees, and enable it to make its escape swiftly and noise-

lessly, when pursued by the natives or by one of the few indigenous birds of prey. It confines itself almost entirely to the food it can find in the earth, especially worms, in searching for which it is greatly assisted by the long beak with its delicate sense of touch. It drives its bill into the soft damp ground, much as the snipe does, and extracts the worms with great skill and precision.

When the species first arose, it was confined to the ground, since nothing was to be gained by leaving it, and the physical structure was therefore adapted to this mode of life, by the gradual elimination of the wings. If the species were only now being formed, the above-mentioned change would most probably not have occurred; for with the invasion of its domain by man, bringing his fire-arms and his cats and dogs, the conditions of life of the Kiwi have been considerably altered, and wings might now stand the helpless bird in good stead. But they have been irretrievably lost, and the race of Kiwis will consequently soon be extinct, like the gigantic ostrich-like birds, the Moas, which are known to have inhabited New Zealand within the memory of man, and the skeletons of which, over twelve feet high, arouse our wonder in museum collections.

As the winged ancestors of the Kiwi adapted themselves more and more to life on the ground in the woods, they came to use their wings less and less, and we may safely conclude that this increasing tendency to disuse of the organs of flight, continuing through long generations, affected the organs themselves, and in some indirect way diminished their size, gradually reducing them to the insignificant appendages we now find.

It is easy to understand how it is that degeneration has gone further in the case of the Kiwi than in that of the ostrich; for, although the latter does not fly, it still uses its wings as aids in running swiftly over the African plains and deserts, while such rapid movement across open country is not necessary for the Kiwi, living as it does in coverts. Short wings with large feathers, like those of the ostrich, would be rather a hindrance than otherwise to the Kiwi in moving quickly through thickets and among underwood, and therefore its wings have been reduced to mere rudiments which are externally altogether invisible.

It is not only among the ostriches that we find degeneration of this kind; certain species of water-birds have become too heavy and awkward to rise into the air, and in these too, for instance in the penguin, the wings are quite useless as organs of flight. But, although useless for flying, they are still of some service for motion in water, and therefore have not degenerated as completely as those of the Kiwi. They have, however, become far smaller than those of flying birds, and, clothed with short scale-like feathers, they bear some resemblance to the fins of fishes.

These few instances will suffice to show that nature is purposeful, not only in adapting recently developed structures to her uses, i. e. in fitting them to perform properly the functions allotted to them, but, conversely, in removing everything superfluous, so that as soon as a structure is no longer required it is eliminated. Of course, this elimination is neither sudden nor voluntary, but comes to pass gradually, in accordance with certain laws, so that we are often able to watch every stage of the transition from the full development of an organ to the entire absence of it.

Such degeneration of once important parts is not only found here and there in nature; it is of frequent, nay, among the higher animals, of general occurrence. It is in fact a natural consequence of the evolution of the higher animals of to-day from earlier and lower forms, which lived under totally different conditions, necessitating the possession of parts and organs, which, in process of time, have been either altered or completely atrophied. If nature had not possessed the power to cause the disappearance of superfluous organs, there could have been no such thing as the transmutation of species; for primitive structures, when they became superfluous, would have been in the way of those in actual use and would have hindered their development. Indeed, had the retention of all original structures been a necessity from the first, the result would have been the production of monsters quite unfit to live. Hence the retrogression of superfluous structures is a condition of progression.

Having found disuse to be the immediate cause of the disappearance of a structure in the course of the development of a species, we may further ask how a structure once essential to

life can fall into disuse. Obviously, this can only happen through a change in the conditions under which the animal lives. When a bird which has been accustomed to seek its food in trees and bushes, finds upon the ground supplies so rich as to afford better sustenance, it will gradually come to live more and more upon the ground, and less and less in trees, a fact which taken alone will entirely alter the conditions of its life. It will not require to fly, and will consequently fly less and less often, and after the lapse of generations will cease to fly altogether. And to bring all this about, the wood in which it lives, the climate, the surrounding animals, need not have undergone any changes; merely the adoption of a new habit by the bird itself will suffice.

It is the same with animals removed from their original habitat; they may find themselves in circumstances so essentially different as to render superfluous some organ which had once been indispensable. For instance, if a species which had always lived in the light, were to find its way into some new habitat where there was complete darkness, its eyes would become useless to it; and accordingly we commonly find that in such species the eyes have more or less completely atrophied.

This is the case, for instance, with animals which live in dark caves. In the limestone caverns of Carniola and Carinthia a blind amphibian, the Proteus, is found in great numbers, and there are also blind Crustacea (both isopods and amphipods), blind insects and snails. In the Mammoth Cave of Kentucky among other blind animals we find a blind fish and a blind fresh-water crayfish. It is almost superfluous to offer any further proof that these species are descended from ancestors which possessed the power of sight, beyond the fact that the caverns in question have not existed from the beginnings of organic life, and that therefore the animals must have lived in the light before they entered them. Nevertheless, in many of these animals direct proof exists in the fact that they still possess vestiges of what have once been eyes. The Proteus and the blind fish of the Mammoth Cave have small imperfectly-developed eyes under the skin, which are no longer of any use as organs of sight. In the case of the blind crayfish, the eyes have entirely disappeared, although the moveable stalks upon which they were placed still remain.

Caves are not the only places where animals are known to live in the dark; in deep wells and at the bottom of the sea and of lakes complete darkness reigns. To Professor Forel of Morges we owe the discovery of the depth to which light can penetrate. Photographic plates were sunk at night to a certain depth, and after being suspended to a buoy, were exposed, for a period of from twenty-one to twenty-four hours, to such light as could reach them. By this means Forel found that even in the transparent water of the Lake of Geneva, the light in winter, when the water is clearest, only penetrated to a depth of 100 metres, and scarcely 50 metres in summer. Later experiments by Fol and Sarasin, with more perfect apparatus and more highly sensitive plates, proved, however, that light penetrates the Lake of Geneva to the greater depth of 170 metres. On a bright day there is about as much light at such a depth as we are accustomed to see on a starlight night, when there is no moon. Below this there is utter darkness; and we find blind animals from these downwards to the greatest depths (300 metres), at which, for example, a blind isopod and an amphipod exist. In the sea, when the water is undisturbed, light penetrates as far as 400 metres, but as we now know that animal life exists in the sea at a depth of 4000 metres, there still remains a vast region in which darkness reigns, and in which numberless blind animals are found,—blind fish, blind crustaceans of various species, blind molluscs and worms. Forms nearly related to all these live where the light penetrates, and possess eyes.

Burrowing animals, too, have, for the most part, either poorly-developed eyes or none at all. Thus earthworms are sightless, while closely-allied pelagic species generally possess eyes, often very highly developed, and of complex structure. The common mole has indeed eyes, although very small ones, completely hidden in its close fur, but in Africa there are moles which are devoid of eyes and therefore entirely blind.

Many other instances might be brought forward to prove that the disuse of the organs of vision results in their disappearance. And the same conclusion holds good for other organs; experience teaches that, as soon as any organ falls into disuse, it degenerates and is finally lost altogether.

We find interesting confirmation of this fact in the other

organs of special sense, although cases of the disuse of these are of less frequent occurrence. Thus the caecilians, tropical worm-like or snake-like amphibians, living underground, have lost not only the sense of sight, but that of hearing also. They possess neither tympanum nor tympanic cavity, and although the auditory vesicle, which is buried in the interior of the skull, still exists, the auditory nerve, which should be in connection with it, supplying its sensitive nerve-endings, has entirely disappeared. The sense of hearing must have become useless to them in their life underground, or the organ would not have degenerated [1]. They are compensated for the want of it by a remarkably keen sense of smell, which is more highly developed in these animals than in any other vertebrates.

Instances are also known of disuse causing degeneration in the sense of smell; thus the whales and dolphins have more or less completely lost this organ which is so highly developed in the rest of the Mammalia.

Retrogression is, however, not always carried so far as to do away with a structure altogether, although this generally happens with the organs of sense, because they can scarcely be adapted to other uses. But not infrequently the degenerating organ can be turned to account in some other way, and then

[1] It is now known that the above statements as to the existence of a rudimentary auditory organ in *Caecilia* are erroneous. Recent researches have shown us that these animals not only possess a complete auditory apparatus, but that it is even more perfect than in other Amphibia. In their splendid 'Ergebnisse zoologischer Forschungen auf Ceylon,' Heft 4, 1890, the cousins Sarasin have given an accurate account of the auditory organ of a caecilian (*Epicrium*), and show that it is very far from being in a degenerate condition. It possesses all the essential parts, the auditory nerve is even larger than usual, and one of the '*maculae acusticae*' present is unrepresented in other Amphibia. These writers even prove that, in addition to the ordinary apparatus, many accessory auditory organs are present in the skin, each of which contains an otolith: these are homologous with the 'organs of the lateral line' of other Amphibia and of fish.

Up to the present time our knowledge of the auditory organ of *Caecilia* has been founded upon the statements of two excellent observers, Professors Retzius and Wiedersheim; but the material at their disposal was restricted to a few badly preserved specimens.

We must therefore maintain that the organ of hearing as well as that of smell has been especially developed in the caecilians as a compensation for the want of eyesight. Those conditions of life that would render the power of hearing useless do not appear to exist. As a result of these recent researches, I am now unable to adduce an example of a rudimentary auditory organ.—A.W., 1891.

retrogression either stops just short of actual elimination, as in the case of the wings of the ostrich, or so alters and transforms the structure as to fit it for new functions, like the wings of the penguin, which aid it in swimming.

The far-reaching effects, on the development of species, of retrogression consequent upon disuse are nowhere to be seen more clearly than among parasitic animals.

Many groups of animals contain certain genera, families, or even whole orders, which live at the expense of other animals, feeding on their blood or tissues, yet not killing them after the manner of beasts of prey. Such are the parasites, some of which only seek their unwilling host when impelled by hunger, and leave it as soon as they are satisfied; while others take up their abode in or upon it, only to be driven thence by its death. The great group of worms includes very many parasites, and they are almost as numerous among the Crustacea. Most crustaceans are free-swimming or actively running inhabitants of the water, especially of the sea, and their food is partly of a vegetable nature and partly consists of living or dead animals; but nearly every order includes some parasitic form, in which the effects of disuse resulting from parasitism are plainly traceable.

A visit to the fish-market at any European sea-port, and an examination of some of the larger fish, will generally lead to the discovery of certain segmented animals firmly attached to the integument, and bearing some resemblance to wood-lice. These parasites, called fish-lice, suck the blood of the fish. They are not permanently fixed, but leave their host from time to time and seek a fresh one. Now these animals exhibit with great clearness the effects of parasitic habits: their legs are short, being no longer required for swimming, but chiefly for holding on by, and the organs of sense also are somewhat degenerate, for parasites scarcely need them. It is, of course, necessary for predaceous crustaceans to be able to distinguish their prey at a distance, and for this purpose they require keen sight and a delicate sense of touch in their antennae; but parasitic forms, when once attached to their host, do not readily leave it, or if they do so, a new host is easily found, since fish are mostly gregarious. Hence in these fish-lice the eyes and antennae have become small and insignificant.

This is, however, but the first step in retrogressive development: more marked effects are witnessed in forms which are more completely and permanently fixed to their hosts. To the same crustacean order belong the *Entoniscidae*, which are internally parasitic upon other crustaceans, especially upon the common shore-crab (*Carcinus maenas*). During their whole life, these parasites never leave the host, nor move from the position they have once taken up within it. They live attached to its liver, sucking the juices; after growing enormously and producing thousands and thousands of eggs, they finally die. It is clear that such a mode of life must render superfluous, and therefore degenerate, many structures which were essential to their free-swimming ancestors. This retrogression takes place to such a degree, and the whole structure of the animal is thereby so modified and altered that they are scarcely recognizable as Crustacea. The characteristic segmentation of the body is entirely lost, and the hard exo-skeleton is replaced by a thin soft skin. The body lengthens to a vermiform shape, acquires peculiar pointed appendages for the reception of the eggs, and becomes colourless, like that of all animals which live in the dark. All these modifications are quite intelligible; the segmentation of the crustacean body facilitates movement, while the hard exo-skeleton serves for the attachment of muscles. The eyes and antennae completely disappear, because the animal lives in darkness, and does not need to see, and because the sense of touch is unnecessary to it after it has once taken up its position. Not a vestige remains of certain mouth-organs which are well developed in allied species; and the legs, of which free-swimming forms have seven thoracic and six abdominal pairs, are reduced in number. The internal organs are also reduced, with the single exception of the ovaries, which increase so much in size that the animal appears like a mere bag of eggs.

It may now be asked how we know this peculiar vermiform being to be a crustacean and an Isopod at all. We know this to be a fact because there are many other parasitic Isopods in which degeneration has not gone so far, and which present well-marked stages of transition from the above-mentioned fish-lice to the *Entoniscidae*. Furthermore, the descent of the *Entoniscidae* from free-swimming forms is clearly proved by

the fact that the young still resemble the latter in the possession of eyes and antennae, segmented bodies, well developed jaws, and numerous legs: in short, in all essential points of structure, they exactly resemble the locomotive forms. The young of the *Entoniscidae* are actually free-swimming organisms, and it is necessary for the perpetuation of the species that they should be so, for how could the parent animal, possessing no organs of locomotion, leave its original host for a fresh one? And yet such a change is essential for the continuance of the species; for in course of time the hosts will die. Under such circumstances the young *Entoniscidae* leave the mother as perfect Isopods, make their way out of the host, and lead a free-moving life in the sea until they find and enter another *Carcinus maenas*: they then undergo a whole series of retrograde changes in rapid succession, and finally attain the remarkable vermiform shape already spoken of. Of course, retrogressive development did not reach anything like this degree at first; it was only attained after the lapse of countless generations, and a passage through many intermediate forms. The original parasitic Isopods lived no doubt, like the fish-lice, attached to the external integument of their host; these were followed by others which took up their abode in the internal cavities of the body, in the respiratory chamber and the alimentary canal. Gradually increasing modification then occurred, as the parasites found their way farther and farther into the internal organs. The *Entoniscidae* are not the most extreme cases of retrogressive development among the parasitic Crustacea; there are species in which not only the legs, antennae, eyes, and segments of the body, but the whole head, and even the stomach, intestines, and mouth disappear; food being taken in through peculiar root-like tubes, which absorb the juices of the host in such a manner as to supply ready made nourishment which needs no digestion. But the *Entoniscidae* afford sufficient proof of the extraordinary effect of the disuse of certain parts in transforming the whole organic structure of a species.

Since we find that disuse of an organ is always followed by its gradual disappearance in the course of many generations, the supposition naturally arises that this decline is the *direct consequence of disuse*, and that the inactivity of an organ is the

immediate cause of its degeneration, a view which has hitherto actually been held, and which at first seems credible enough and even plausible.

It is, of course, a well-known fact, although perhaps the subject has hardly been sufficiently studied, that parts which are much used grow larger and more powerful, while those which are seldom exercised become small and weak. Constant gymnastic exercise will immensely increase the size and strength of the muscles of our arms; while these limbs will lose what strength they once possessed if the muscles are never exerted. The performances of athletes afford us the best examples of the extent to which practice can increase the muscular strength and activity of man; and, on the other hand, those who work at occupations entailing a sedentary life and lack of exercise plainly show the weakening effects of disuse. Experiments prove this still more clearly: when the nerve supplying a muscle is cut, degeneration of the muscle ensues, because its activity is at an end, and the same thing happens with glands, when their functions are disturbed by severing the nerves which supply them. We may accept the general proposition that an organ may be strengthened by exercise, and weakened by a long continued state of inactivity. It is not necessary here to go into the question of how this is brought about, nor has it been as yet completely explained: it is sufficient for our present purpose to know that such is the case.

Since we may take it for granted that disuse of an organ will lead to its degeneration, even in the life-time of a single individual, may we not also conclude that the gradual disappearance of a superfluous structure in the course of generations is due simply to the tendency to degeneration being handed down from one generation to another, and thus gradually intensified to the extent of complete elimination? For supposing disuse to produce infinitely small effects during the life of each individual, yet surely these effects would be cumulative, and in course of generations the organ would gradually diminish in importance, become smaller and weaker, and ultimately disappear altogether.

This explanation, obvious as it may seem to be, cannot be the right one, for there are many facts which are quite incompatible with it.

In the first place, it compels us to assume as a fact what has often been asserted, but never yet proved, viz. *the hereditary transmission of acquired characters.*

It is well known that many mental and physical qualities of parents are transmitted to their children, such as the colour of the eyes and hair, the shape and size of the finger-nails; and not only these but, as everyone knows, even such minute and indefinable physical and mental characteristics as likeness of features, bearing, gait, handwriting, a mild and equable or passionate and irritable temperament. But all these characters are blastogenic, or inherent in the parents; whether they first show themselves early or late, they have existed in the parents in a more or less marked degree and in different combinations, from the beginning. Characters only acquired by the operation of external circumstances acting during the life of the individual, cannot be transmitted. The loss of a finger is not inherited; all the thousand faculties which are gained by the exercise of various organs or of the whole body are purely personal acquirements, and are not handed down to posterity. No case was ever known of a child being able to read without being taught, even though the parents had exercised their faculties in this direction all their lives. Children do not even learn to speak untaught, although not only their parents, but countless generations of ancestors, have exercised and perfected the brain and vocal organs by learning and speaking a language. It may now be considered as satisfactorily established that children of civilized nations, if brought up in a wilderness and cut off from all communication with man, would make no attempt at speech. For proof of this I need not fall back on the not very well authenticated story of the Persian monarch, who is said to have made the cruel experiment of taking twenty new-born children and bringing them up together, without ever allowing them to hear a word of human speech; they are supposed never to have made any sound resembling speech, but to have imitated with great fidelity the bleating of a goat which lived among them. The same thing is told in all the well-known cases of young or adult persons found living in an utterly wild state in the woods, cases which have occurred from time to time up to the last century in Germany, France, England and Russia. Nearly all

these persons are said to have uttered sounds resembling the cries of wild animals with which they had associated, but not one was ever known to speak. When we consider the constant and unremitting practice in speech which we gain in a life-time, whether by speaking aloud or merely by thinking to ourselves, and remember that in spite of the effect of this perpetual exercise for centuries upon the human brain and vocal organs, —the power of speech has not become in the slightest degree fixed or intensified by heredity, I think that we are justified by this one fact alone in altogether doubting whether acquired characters can ever be transmitted in any real sense. Moreover their transmission is quite incompatible with the only theory of heredity which seems to me to be tenable.

But if the results of the exercise of an organ are not inherited, neither can the effects of disuse be handed down. Hence, if this be true, the retrograde changes taking place during the lives of individuals cannot possibly be intensified in the course of generations; for the process of retrogression would have to begin afresh in each generation successively, and thus would never advance any farther than it did in the individuals of the first. We must, then, regard this supposition that degeneration is caused by mere disuse as a mistaken one, and seek a more satisfactory explanation of the facts. I think, moreover, that such an explanation is to be found in what may be called reversed natural selection.

To state my meaning more clearly, Charles Darwin and Alfred Russel Wallace have taught us to understand by 'natural selection' that process of elimination effected by nature itself without the aid of man. Inasmuch as far more individuals are born than can possibly live, only the best are enabled to survive, the best being those which are so formed as to be the 'fittest,' as we say, for the conditions of life in which they are placed. As in each generation only the fittest survive and propagate the species, their qualities only are transmitted, while the less useful qualities of the weaker individuals die out. Each successive generation will therefore consist of individuals better organized than those of the preceding one, and thus useful characters will be gradually intensified from generation to generation, until the greatest possible degree of perfection is reached. Probably this theory

is far from new to many of my readers: it has been so often explained in various well-known works and periodicals, that any further elucidation is unnecessary.

What holds good for the individual as a whole also holds good for each separate organ, inasmuch as the ability of an animal to perform its allotted functions depends on the efficiency of each particular organ: hence, by means of this perpetual elimination of the unfit, every organ is brought to the greatest perfection. On this hypothesis, and on this only, is it possible to explain the wonderful adaptability of the minutest details of structure in animals and plants, and the development of the organic world through the operation of natural forces.

If this view be the true one, if adaptation in all the parts of living forms be truly the result of natural selection, then the same process which produced these adaptations will tend to preserve them, and they will disappear directly natural selection ceases to act. These considerations show why organs which have become superfluous and have fallen into disuse necessarily degenerate and ultimately disappear.

As an example of this, let us take one of the newts, which are so common in our swamps and pools in spring. If we examine its eyes we find that they are not very large, but very highly developed: their structure bears considerable likeness to that of the human eye, and they play a very important part in the life of the animal, which is almost entirely dependent on keenness of vision for finding its prey. It detects at once and snaps at anything in motion: were it not for its eyes, it would infallibly starve. Now these eyes are extremely delicate and complex organs, which have only very gradually,—i. e. in the course of countless generations and of almost endless time,—reached the degree of perfection attained by them in the living newt. The whole series of developmental stages is not indeed known to us; but in other groups of animals we find eyes at every grade of development, and from these we can form some idea of the way in which the gradual improvement of an original simple and imperfect eye took place. The slow but steady progress in development from stage to stage is due, as I believe, to the fact that the eyes of these animals were never all exactly alike, nor all equally keen, and that only those individuals survived in each generation in which the develop-

ment of the eyes was above the average. This process of natural selection would not only gradually produce improvement in the eye, but would also tend to keep the improvement, when gained, up to a certain standard.

Now suppose such a species to have been carried underground by water into a dark cavern. It would only gradually adapt itself to the new conditions and thus be enabled to thrive in the cave: but after the lapse of generations the individuals would have learnt to live in complete darkness, and to distinguish and catch their prey without the aid of sight, and this would be rendered possible by an improvement in other organs, especially those of touch and smell. Thus in course of time a race of newts would be produced perfectly adapted for life in the dark, and for finding food by scent alone and not by sight; and this race would make its way farther and farther underground, and pass its whole life in utter darkness. It is in some such way as this that not only the entrances of caverns, but whole series of caves, connected by subterranean streams, rivers and lakes, like those in the Karst Mountains, near Trieste, have come to be tenanted by animals.

Directly, however, such cave-dwellers became able to exist without using their eyes, degeneration of these organs would set in: as soon as they ceased to be essential to the life of the animal, natural selection would be powerless to affect them, for it would be immaterial whether the eyes of any animal were above or below the standard. Hence the individuals with weaker sight would no longer be eliminated, but would have an equal chance of surviving and propagating their species. Crossing would then take place between individuals with strong and weak eyes, and the result would be a gradual deterioration of the organ. Possibly the process might be accelerated by the circumstance that small and degenerate eyes would be rather an advantage, because their decrease would involve an increase in the powers of other and now more important organs, such as those of touch and smell. But even independently of this, the eye, directly it ceases to be kept up to a certain standard of development by natural selection, will gradually deteriorate, the process being very slow at first, but absolutely sure.

The same simple explanation suffices for *all* cases of retrogressive development, whether of organs or species. On any

other theory many facts are incapable of explanation, even assuming the possibility of the hereditary transmission of acquired characters, such as those produced by disuse.

It is clear that degeneration as a result of disuse can only take place in an organ the activity of which depends upon its exercise, so that a real effect is produced by the discharge of function. The act of seeing involves certain chemical changes in the retina of the eye, and perhaps even in the optic nerve, processes which do not take place when the eye is no longer exposed to light. Flying involves metabolism in the muscles which move the wings, and this also ceases when flight is at an end. So that an actual retrogressive influence is exerted on certain parts of the eye and on the muscles, by disuse. But how can the stamens of a plant be affected by the failure or success of their pollen in finding its way to the stigma of another flower? Yet we know that hermaphrodite flowers sometimes revert to the original condition in which the sexes were separate, and this by the gradual atrophy of the stamens in one flower and the style in another. Whether this particular case is to be explained by the cessation or by the active operation of natural selection, is another question, which we may proceed to consider.

After the anthers, in the course of evolution, have withered away and disappeared, their stalks (the filaments) remain, and are often of considerable height and thickness. Slowly and very gradually these degenerate also: we find them quite long in some species, in others short, while in others again they have completely disappeared, only reappearing now and then in single instances to remind us that they were once of normal occurrence. It is true that the filaments are no longer useful, but how can this fact have any direct effect in causing them to degenerate? Their structure remains the same, the sap circulates in them as before and supplies nourishment to them as well as to the petals and the style. From my point of view the matter is intelligible enough; for the bare filaments which have lost their anthers are in no way essential to the life of the species: natural selection is powerless to affect them and they gradually degenerate.

Even more striking instances are to be found in the animal kingdom. Why have most of our domestic animals lost their

original colouring? Clearly because colour became of little or no importance to them as soon as they were sheltered under the protection of man, while in a wild state it was a great safeguard against detection by their enemies.

Similarly the hairy covering has ceased to be of importance to certain of the Mammalia—and has disappeared. Thus whales and dolphins have a naked skin for the most part entirely devoid of hair, although they are unquestionably descended from hairy ancestors, and even now rudimentary hairs may be detected in certain parts of the body by the aid of the microscope. Obviously, the disappearance of the hairy covering cannot be a direct consequence of disuse, for hair will grow as well, whether its protective warmth be useful or of no importance to the animal. But its disappearance as an indirect consequence of disuse is plain; for as soon as an immense thickness of blubber was developed beneath the skin of the whale, the warmth of an additional covering was unnecessary: the hair becoming superfluous, natural selection ceased to affect it, and degeneration at once set in. If anyone is inclined to doubt whether the direct action of sea-water may not have caused the disappearance of the hair, it is only necessary to point to the group of seals, in which all the smaller species possess a thick coat of fur, while, among the larger kinds, the walrus has but a scanty covering of bristles, because, like the whale, it has developed a layer of blubber, which is amply sufficient to protect its huge body from cold.

Examples of an entirely different kind are afforded by those animals which hide themselves in cases or houses. The hermit-crab partly conceals itself in empty shells, the aquatic larvae of caddis-flies (*Phryganidae*) build cases within which their cylindrical bodies are enclosed, and the larvae of certain small moths (*Psychidae*) do the same. Whenever the body of any such animal is thus partially enclosed in a case, the protected parts are soft and whitish, i. e. more or less colourless, while the exposed parts retain the ordinary hard integument of the Arthropoda and are variously and strongly coloured. Now we may maintain that, in a certain sense, the hard integument of crabs and insects fulfils the 'function' of protecting the soft parts of the animal from injury, but, correctly speaking, this defence is not a real function at all, because the exercise of

function implies activity, while the use of the hard integument can only be of a passive kind. The horny covering itself is not in the least affected, whether it is useful or useless as a defence against stings and bites : such assaults are quite immaterial to it, nor does its condition in any way depend upon the frequency or rarity of attack. Degeneration cannot, then, be the result of the protection afforded to the integument. Inasmuch as the integument of all the three kinds of animals mentioned above only degenerates in those parts which are protected by the case, clearly the only explanation must be that the hard covering is unnecessary for those parts which are otherwise protected, and that consequently natural selection has no power to preserve it.

But the most striking instances are to be found among the social insects, especially the ants. The male and female ants are winged, and at certain times of the year rise into the air in great swarms. Everyone must have seen these swarms filling the air in summer and autumn : they may often be seen on the top of a hill, or surrounding the summit of some tower, alighting on walls and parapets or covering the hats and clothes of people. The males and females, however, form the minority in an ant-community, the greater number being workers—the common wingless ants. Now these workers, in the course of the development of the species, have forfeited their wings as a consequence of disuse, because the power of flight would be useless to them, and they would be exposed to even greater dangers in the air than on the ground. The business of their lives is to forage for food-supplies, and to collect building materials for the nest, but everything which they seek is obtainable on the ground : they have also to feed the larvae and tend the pupae, and to them alone belongs the defence of the nest if attacked. All these tasks bind them to a life on the ground ; hence, when in former days, they were being gradually developed from perfect females, they came to use their wings less and less, as they gave themselves up more and more completely to the duties allotted to them. Now, in this case also, it would at first sight seem probable that the long continued disuse produced a certain amount of degeneration in each individual, that this first retrograde change was inherited by the succeeding generation, and gradually intensified by further disuse, and so on. Such a view is, how-

ever, entirely disposed of by a fact which admits of no dispute and cannot be explained away, viz. *the fact that the workers of ants are infertile, and do not propagate their species.* Consequently, it is impossible that the degeneration caused by disuse during individual lives should be handed down, and the elimination of the wings is only explicable on the other theory, which ascribes it to the cessation of the operation of natural selection which ensued when the wings became useless and of no importance. It may certainly be objected that the disappearance of the wings might have taken place before the workers became infertile; but such a supposition cannot be accepted, for reasons which I need not enter upon here. The infertility of workers may also be regarded as a difficulty from my point of view, but it must be remembered that the principle of the elimination of the unfittest does not act directly on the workers, but on their parents, the propagators of the species. In other words, natural selection does not affect the workers themselves, but the parents, and determines their survival according as they produce perfect or imperfect workers.

The process by which the degeneration of superfluous organs takes place may fittingly be called 'universal crossing' (Panmixia), because it implies that not those individuals only in which any particular organ is best developed survive and propagate their species, but that survival is quite independent of the efficiency or non-efficiency of the organ. This process of Panmixia must have had, and must have still great influence on the development of the organic world. The changes wrought by evolution have been and are innumerable, and they by no means always occur in an upward direction, but often—as shown in the case of the parasites—in a downward one, or perhaps most frequently in both directions at once, the change being retrogressive in one part and progressive in another. And very often the former change may actually lead to the latter. We ourselves could hardly have attained so high a degree of intellectual development, had we not forfeited a considerable share of the physical advantages possessed by our remote ancestors. The savage tribes which depend upon the chase, are gifted with a much keener sense of hearing, smell, and sight than we are, and this is not merely the result of constant training, but is also due to the inheritance of more

efficient organs. In this respect civilization has caused degeneration in us, by means of Panmixia, owing to the fact that the well-being of individuals no longer depends upon the highest possible development of their sense-organs. At the present day we are able to make a living equally well, whether our sense of hearing or smell is delicate or the reverse, and even keenness of sight is no longer of decisive importance to us in the struggle for existence. Ever since the invention of spectacles, short-sighted persons—in the higher classes at any rate—experience hardly any greater difficulty in getting a living, than that endured by people with keen sight. In former times a short-sighted soldier or general would have been a sheer impossibility, and so would a short-sighted hunter: in all grades of society short sight used to be a very real disadvantage and an almost complete bar to advancement of any kind. This is no longer the case now; a short-sighted man makes his way in life as successfully as any other, and his defect, if congenital, will be transmitted to his children, and will therefore tend to make hereditary short sight commoner among certain classes. Of course short sight may also be an acquired character, and in such cases it is, I venture to affirm, not transmitted. But I believe that the great prevalence of short sight is not only due to the injuries acquired by over-straining the eyes and continually looking at near objects, but also to Panmixia, or cessation of the action of natural selection,—a law to which we are naturally subject in common with other animals.

Much might be said of the effects of civilization in causing physical degeneration, which indeed appears to be on the increase. Consider for a moment the teeth: the art of dentistry has been brought to such a pitch of perfection, that artificial teeth are now almost to be preferred to natural ones. At any rate no one need die now from insufficient nourishment in consequence of the inability to masticate food, and there is nothing to prevent the transmission of a predisposition to bad teeth to any number of descendants.

Nevertheless we need not fear that civilization will ever lead to utter degeneration in man. The antidote is to be found in the very process which causes the first deterioration of an organ; for obviously such deterioration can only continue as long as it is not injurious to the individual in the struggle for

existence, and when that point is reached natural selection will interfere to prevent further degeneration. To return to our former example, it is quite conceivable that the percentage of persons with hereditary short sight may steadily increase, without seriously affecting the general standard of vision of mankind as a whole, or even that of a single nation or class, because degeneration below a certain point would become a fact of decisive importance to the individual, leading to failure in the struggle for existence. Thus we need not fear the complete loss of our eyes through degeneration, like that which has affected the animals living in the dark and the above-mentioned parasites; and we need not anticipate any serious diminution of our muscular strength, or powers of endurance, or many other qualities.

Hitherto I have only treated of the degeneration of physical characters in consequence of disuse and Panmixia, but the same thing takes place with mental qualities, a fact which need not surprise us when we remember how close is the connection between all mental and physical processes, how the relative size and complexity of the brain is a measure of the degree of intelligence, and how every instinctive action of an animal presupposes a corresponding arrangement of the nervous system which compels a certain action to follow upon a certain stimulus. Hence degeneration of an instinct in an animal must always have been preceded by degeneration of that network of nerve-cells and nerve-fibres in the brain in which the instinctive action had its rise. Retrogression, then, in physical structure is not antagonistic to retrogression in instinct and mental faculty, but mental and physical degeneration rather go hand in hand. Very definite and extensive physical degeneration always implies a corresponding mental deterioration. Those *Entoniscidae* which have lost their eyes, antennae, legs, and jaws, have also degenerated in intelligence, as is but natural in animals which only require to remain still and imbibe nourishment: the whole nervous system of these Crustacea has been reduced to a remarkable degree.

Certain examples are most interesting as tending to prove that retrogression may be confined to one particular instinct, leaving the animal and its powers as a whole quite unaffected. The loss by domestic animals of the instinct to escape is one of

these examples. Almost all wild animals, mammals as well as birds, possess the instinct to escape: they are not only extremely attentive to the slightest sound and smell, and to every movement taking place within their field of vision, but all of them, the predaceous animals not excepted, are continually mindful of their safety, and though not always consciously on the watch, are so to a great extent instinctively. A wild bird flies away at the least sound; a hedgehog which has been surprised, and has rolled itself up, only unrolls itself to run away after the lapse of a considerable time, while the slightest suspicious sound will make it roll up even more tightly. These acts are not the result of reflection, but are purely instinctive, the act of rolling-up being always associated with the perception of sound, so that the former follows instantaneously upon the latter, before the animal has had time to reflect on its meaning, just as we shut our eyes the instant that anything touches them. In the higher animals these movements are certainly under conscious control, i. e. they are capable of suppression, and hence it is that animals in a state of captivity lose the instinct of being startled and of escaping. This instinct is nevertheless deeply implanted in them, and many generations must be passed in domestication before the natural timidity is lost. I believe that the loss is brought about by cessation of the action of natural selection, and a consequent gradual degeneration of the instinct. Of course it is difficult to judge of the amount of influence exercised by custom upon the life of the individual, but it may at least be considered as certain that the young of our domestic fowls, geese, and ducks, have lost much of the instinct to escape possessed by their wild ancestors, and that they would never become quite wild again even if placed under the care of a wild mother from the first.

The length of time which may be necessary before domestication can get the better of this passive kind of wildness, as the instinct to escape may be called, is seen in the case of the guinea-pig. These animals have been domesticated ever since the discovery of South America about 400 years ago,—a period of time which has not sufficed to overcome their natural timidity. Any loud noise will make them start violently and seek to escape, although they may never in their lives have had any experience of real danger: even shortly after birth the same

thing will happen. In these, as with the various species of pheasants which have been domesticated, the young animals are the wildest: the instinct to escape has been inherited almost unaltered, and the process of taming must begin afresh with each individual. The tameness of the adult animal is here still an acquired character, i. e. one acquired during the lifetime of the individual, and is not inherent, or rather, it is not the result of those changes in the potentialities of the germ which are gradually produced by universal crossing. The tameness comes about just as in wild animals taken young, such as foxes, wolves, rats, or finches, all of which are tameable up to a certain point, and become accustomed to the absence of enemies.

It is also interesting to note that loss of the instinct which impels animals to seek their food may sometimes occur. Both food itself and the power of obtaining it are essential to life, and the instinct of seeking food may be looked upon as the first and earliest developed of any: yet it may be partially or even entirely lost. The young of many birds no longer possess the instinct; they open their bills and cry, and they swallow food placed in their mouths, but they have no idea of picking it up if scattered on the floor of their cage; the sight of food does not result in any impulse to eat. At this early period of life such birds have not learned the art of feeding themselves, and this is not unnatural; for they leave the egg in a very undeveloped condition, and their parents feed them by putting food into their mouths. A part of the food-seeking instinct has thus become superfluous and has disappeared. It may be objected that the little creatures are too undeveloped to feed themselves; this is true, and it is the reason why the parents feed them and why their instinct is undeveloped. But many other birds, fowls, for instance, run about directly they are out of the egg and pick up food for themselves; here the food-seeking instinct is unimpaired.

One of the most remarkable cases of degeneration of the food-seeking instinct is found in certain ants. It has been known ever since the beginning of this century that some species of ants keep slaves, for instance, the reddish ant found in the meadows of Switzerland and Alsace (*Polyergus rufescens*). It is not a large but a strong species, which has adopted the

habit of sallying forth in troops from time to time, to make raids upon and plunder the nests of some weaker species, such as the common *Formica fusca.* The object is, however, not to destroy or devour the ants they attack, but merely to carry off the pupae to their own nest, where they receive every care: the workers hatched from them are then employed as servants, or, to use the usual term, as slaves. These slaves, fulfil all the duties of the nest, which would otherwise have fallen to the share of the red workers; they feed the larvae, build galleries and chambers, bring in food-supplies, and even feed their lazy masters! This is no fable, as was once thought, but an ascertained fact, proved to be such early in this century by Huber of Geneva, a celebrated observer of ants, and since fully confirmed by his pupil and successor Auguste Forel, as well as by Sir John Lubbock. I have also convinced myself of the truth of the assertion.

The most curious part of it, however, is that, in consequence of being constantly fed by their slaves, the red ants have entirely forgotten how to procure food for themselves. If they are shut up and supplied with honey, which is their favourite food, they will not touch it, but will suffer hunger, become weak and feeble, and ultimately die of starvation, unless pity is taken upon them and they are given one of their dusky slaves. Directly this is done, the slave falls to work, eats a quantity of the honey, and then proceeds to feed its masters, which are perfectly willing to be saved from starvation in this manner.

Here, then, as in the case of nestlings, the food-seeking instinct and the power of distinguishing food by sight have degenerated, and clearly in consequence of disuse. Inasmuch as a colony of red ants always owns plenty of slaves, the food-seeking instinct has become unnecessary, natural selection has ceased to affect it, and it has gradually died out. Other instincts too have been lost by these red ants in consequence of their habit of keeping slaves; they have quite forgotten the art of nest-building and in part that of tending their young. Other species of ants devote much attention to their pupae, moving them about the nest from time to time, and often carrying them out into the air and sun, and they feed their larvae with the greatest assiduity. But the red slave-making

ants have no such instincts; they care nothing for their own young, and the species would become extinct, if they were suddenly deprived of their slaves. So it is not only among men, that there is a curse upon slavery; even animals become degraded by it.

Other species of slave-making ants are known, and have been carefully studied, in which the degeneration of the masters goes even farther and affects their physical strength. But so much remains unexplained in the life-history of these species, that I will not treat of them here, remarkable as are the observations which have been made about them. All these examples afford further support to our theory of retrogressive development as a result of disuse; for the above-mentioned cases of the degeneration of instinct took place in worker-ants, i. e. in animals which have not the power of propagating their species. Hence the disappearance of the instincts in question cannot be due to the hereditary transmission of any degeneration acquired by individuals in consequence of the fact that they were not required to seek their own living.

In the cases above quoted, the instinct of feeding has not entirely degenerated, but only a part of it has been lost, viz. the instinct of seeking food and the power of recognizing it by sight. Evidence is, however, forthcoming to show that the whole instinct of feeding is sometimes lost, so that actually no hunger is felt and no nourishment taken. This may sound very strange, but it is an undoubted fact that there are animals which absorb as much nourishment in the larval stage as will last them during the rest of their life. Many moths, especially among the Bombyces, possess very degenerate mouth-organs, and so do the *Ephemeridae*: all these take no sort of food. In male Rotifers the alimentary canal is entirely wanting; they have neither mouth, stomach, nor intestine; their lives are of such short duration that the food material with which they begin life is sufficient to sustain them throughout it. There is no luxury in nature; no instinct and no organ in the body can persist unless absolutely essential to the life of the species. Panmixia—in other words, the cessation of the operation of natural selection—removes all that is superfluous, only leaving that which is absolutely necessary.

But, of course, if our theory be the right one, such retro-

gressive development can only take place very gradually: it must require many generations to completely eliminate what is superfluous, and we should expect to find in many animals vestiges of organs and structures once significant, but now on the road to complete obliteration. And this is actually the case, as I have shown above. So-called 'rudimentary' organs are present in numberless cases, and in various animals, and give us some idea of the vast amount of change which every species must have undergone in the course of ages. Of such a kind are degenerate eyes, hidden beneath the skin, as in the Proteus, the golden mole, and the *Caecilia*; the rudimentary wings of the Kiwi, and of many female moths the males of which have well-developed wings; the almost invisible projections near the mouth of the *Ephemeridae*, which are nothing less than degenerate jaws; and a thousand other examples. To the same causes are due the numerous cases in which an organ, fully developed in the ancestors, is wanting in the adult descendant, although present in a rudimentary condition during youth or embryonic life. Thus, the workers of ants are, as before mentioned, wingless, but the vestiges of wings are still to be seen in the larvae, in the form of small disc-like objects beneath the skin, which subsequently disappear. Thus, too, the larvae of bees have lost their legs, because they do not need to crawl about, but live enclosed in a waxen cell in close proximity to their food: although disuse has thus brought them to the condition of footless grubs, in the egg they nevertheless still exhibit vestiges of the legs which their saw-fly-like ancestors must have possessed. Examples like these show that retrogression in an organ, which degenerates from disuse, takes place first in the mature stage, and does not extend to the embryonic stages until much later. An organ may persist in the embryo for thousands of generations after it has been eliminated from the adult organization. The history of evolution affords many well-authenticated instances of organs which persist in a rudimentary condition and never attain a higher development. They are, of course, of the greatest importance as throwing light upon the past history of a species, and are in themselves sufficient proof of the number and diversity of the ancestors of existing species; they show us how intricate and devious are the workings of nature in the evolution of the organic world—now progressive, now retro-

gressive, now concerned with the development of a single structure, and now of a whole organism. Everything that nature has built up with such elaborate care—highly-developed organs of locomotion, limbs fitted to support a certain weight, joints with their complex and yet easy movements, the exquisite balance of muscular strength required for rapid motion on the ground, wings adapted for flying, with all the marvellously adjusted organs which overcome gravity and render rising into the air a possibility, every one of the adaptations by which animals are placed in communication with the outer world which surrounds them,—eyes of the most delicate and complex structure, organs of hearing and smell so wonderfully formed that it has needed long years of the combined researches of all the most eminent naturalists to understand their full significance—each one of these is relinquished, is handed over to a process of gradual destruction, the moment it ceases to be essential to the life of the species.

It would indeed seem as if such a process of development could not justly be called progress, and as far as the individual organ undergoing degeneration is concerned the process is of course retrogressive; but the case becomes different when we regard the organism as a whole. For the end and purpose of all living beings is after all but the existence of each individual: the form assumed, the complexity of structure, the degree of perfection, are all quite immaterial provided that the species be fit to survive: less than fit it cannot be, or it succumbs, neither can it be more so, because no means exist which can enable it to rise beyond the point of fitness necessary for survival. Schopenhauer's pessimistic view that the world was as bad as it could be, and that, if it could grow in the least degree worse, it would be annihilated altogether, might be reversed and converted into an optimistic one: for it would be equally true to say that the world is as excellent as it is possible to make it with the given materials, and that a nearer approach to absolute perfection is inconceivable. The organic world teaches us that such is the case; each existing species shows the purpose of its being in every detail of its structure, and in its perfect adaptation to the conditions under which it lives. But it is only adapted so far as is actually necessary, only so far as to make it fittest to survive, and not a step further. The eye of

the frog is but an imperfect organ of vision as compared with the eye of the falcon, or that of man, but it is perfect enough to enable it to see the crawling fly or the writhing worm: it suffices for the needs of the species. Even the eye of the falcon is not absolutely perfect as an organ of vision from a purely optical point of view, but it serves to enable the bird to distinguish its prey with certainty from a great height: such a pitch of perfection is all that is essential for the life of the species, and all possibility of higher development of the eye, by means of natural selection, is therefore precluded. The object of all evolution, viz. the survival of the fittest, is not, however, always and only attained by the ever-improving, progressive development of the organism as a whole, or of particular organs: new possessions are not invariably added to the old, but the latter are often rendered superfluous in the course of time and taken away. Nor does this happen in an ideally perfect way, suddenly, as if by magic, but slowly, in accordance with existing laws, so that the process remains uncompleted through long ages. But ultimately the organ which is no longer essential to life is done away with altogether, and the balance between the structure of the body and its functions is restored, so that, in this sense also, retrogression may in truth be said to be a part of progress.

X.

Thoughts upon the Musical Sense in Animals and Man.

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X.

THOUGHTS UPON THE MUSICAL SENSE IN ANIMALS AND MAN.

Modern biology depends, as everyone knows, upon the hypothesis of a gradual transformation of all forms of life—the hypothesis of the origin of species by the slow process of evolution, not by a sudden act of creation. Furthermore, most people are aware that biological science holds the chief agent of this transformation to be the principle of natural selection, discovered by Charles Darwin and Alfred Russell Wallace. Out of the vast number of offspring born into the world in each generation, only a very small fraction can survive long enough to become the parents of the succeeding generation; the rest perish from the attacks of enemies, from the inclemency of weather, from hunger or thirst,—in short, they succumb in the struggle for existence. No two individuals are exactly alike, but every one differs in certain respects from all the others: such differences sometimes increase, sometimes diminish the power to succeed in the struggle for life. Those individuals which possess an increased power of resistance will, as a rule, survive and produce offspring, whether their advantage be due to greater muscular strength, keener senses, thicker fur, greater speed or power of flight, &c. This selective process being repeated in each generation, so that only those individuals which possess qualities the most helpful in the struggle for life, are enabled to become the parents of offspring, it follows that such qualities will gradually spread over all the individuals which make up the species and will grow until they have attained the highest perfection.

In this way is explained the evolution of every useful quality and the adaptation which is so manifest in all living beings.

It is, however, very probable that the animal world is also subject to a selective process of another kind,—the sexual selection of Charles Darwin. I will devote a few words to this principle, inasmuch as our main subject is immediately connected with it.

We are all familiar with the song of the grasshopper and cricket. If one walks in the meadows along a little brook on a fine June evening, he will often hear a long-sustained note, even, subdued, and pleasant, which vibrates powerfully without swelling or diminishing, somewhat like that of the nightingale in Haydn's 'Toy Symphony.' A cautious approach will enable us to see a mole-cricket sitting, apparently motionless, in front of its hole in the ground. More careful examination proves that the short wing-covers are in a state of continual vibration, producing friction as they move; and this it is which causes the sound. The microscope shows that minute and delicate teeth are placed at regular intervals along a vein on one of the wing-covers; when these are struck at a certain rate by a vein on the other wing, they emit a whirring note of a definite pitch. One vein acts as the bow, the other as the string of a violin; the mole-cricket is a violinist, and can therefore hold on its note as long as it will.

It is evident that the power of producing a song can be of no value to these animals in the struggle for existence. It neither helps them to find food, nor defends them from their enemies: it is therefore impossible that it can have arisen by the operation of natural selection. Furthermore, when we enquire into its mode of origin we must take into account the fact that only the males possess the gift of song. This is also true of all other singing insects, such for instance as grasshoppers. The ancient Greeks were aware of this, for Xenarchus, in one of his comedies, says, 'Are not the cicadas happy, whose wives have not got an atom of voice[1].'

Here then we find the solution of the problem; the origin of the sound-producing apparatus receives a simple explanation in the contest between the males for the possession of the females. If we take it for granted that the females are pleased

[1] Εἶτ' εἰσὶν οἱ τέττιγες οὐκ εὐδαίμονες Ὧν ταῖς γυναιξὶν οὐδ' ὁτιοῦν φωνῆς ἔνι;

by the song—and this may be accepted as proved,—we can understand the development of an at first imperfect musical apparatus out of the primitive veins of the wing, and its gradual improvement up to its present condition. The females must, at all times, have preferred the males that sang the best: this being the case, according to the law of heredity, the best developed apparatus was, in each generation, transmitted to the males of the next, so that a gradual improvement in the power of performance must have taken place. The continued preference for the best singers necessarily led to improvement in song and in the sound-producing organ, until the latter became incapable of further improvement.

Let us now briefly consider the song of birds. Here, too, the power of song is possessed by the males alone, and its origin cannot be explained by natural selection, inasmuch as it does not help in the preservation of the species, but is rather disadvantageous, for it betrays the presence of the little creatures to their enemies at a distance. But it can be well explained by sexual selection. The males that sang the best being always preferred by the females, we can understand how out of the primitive chirp a kind of song arose in the course of generations, and how, in certain species, it became more and more complex, until at length it developed into songs which delight even man by their beauty, such as those of the linnet, the blackbird, and the nightingale. Hence sexual selection affords a sufficient explanation of the origin of song in birds and insects.

But how can man have acquired the power of making and understanding music, and how can we conceive of the agents by which such a faculty has been developed?

Can these agents be found in the processes of natural and of sexual selection? Undoubtedly man is as completely subservient to the influence of natural selection as any other animal or plant. Man, like every other organism, is variable, is bound by the laws of heredity, and wages a constant struggle for existence. Therefore, with him as with them the qualities which aid in that struggle will be retained and improved, while those which are disadvantageous will be lost. And this *is* natural selection.

It is impossible to doubt that the intelligence of the human

species has been largely increased since the days of primitive man. Intelligence is man's chief weapon,—a weapon which must have been as important for his existence as physical qualities, and this too even in the most primitive times. Think, for instance, of a race that depends solely upon the products of the chase. In such a case, not only are keen senses and bodily strength and endurance essential for the existence of the individual, but he also needs intelligence, cunning, and astuteness in hunting game; boldness and the gift of working in combination in conquering enemies; wise foresight in preventing starvation during unfavourable seasons. Any improvement in these qualities must have given the possessor a greater chance of survival and of leaving offspring. Hence these beneficial attributes would be slowly intensified in the course of generations: the average degree of intelligence would continue to increase so long as the difference between life and death, between failure and success in begetting offspring, was determined by its means.

There can be no reason why this gradual increase in the human intellect should not be going on at the present day: it would at least be difficult to bring forward conclusive arguments against such an opinion. It must be granted that, even under the conditions imposed by modern civilization, the highly intelligent man, in any calling, has, *ceteris paribus*, more chance of founding a family than one with less intelligence. If this be true, although only when large numbers are considered, it must also follow that the average of very many cases would show that the mental power of man is increasing, although very gradually. It is quite true that we fail to detect any historical evidence of this progress, when, for instance, we compare the Greek and Latin poets and philosophers with those of our own day. But this fact does not conflict with the argument, for the leading nations of the present day are not descended from the ancient Greeks. The development of mankind does not proceed along a straight road, but a very interrupted one. The intellectual achievements of the ancient Greeks did not pass into their descendants, but into the Romano-germanic nations, and these only received the intellectual achievement, and not the intellectual power. It is also to be noted that an increase in the intelligence of mankind may

not only take place by a rise in the greatest heights attained by human intellect, but also by a rise in the general average.

We will now leave this aspect of our subject: my object was merely to show that the human intellect must have been improved during many thousands of generations by the process of selection, and this can hardly be doubted.

A very different answer must be given if we ask whether it is possible to conceive of a similar origin for every kind of talent and faculty possessed by civilized man, if we enquire whether the musical, artistic, poetic, and mathematical talents can have originated in a similar process of selection. It is clear that they did not arise in this way. Such talents may, now and then, have been useful or even of decisive importance in the struggle for existence, but as a rule they are not so. And no one will be prepared to assert that musical or poetic gifts mean an unusually good chance of founding a family, although this is perhaps more nearly true to-day than it was in the times of Schiller, Haydn, and Mozart, or still earlier. But even to-day the man with a practical turn of mind stands a greater chance of material success than one whose talents are of a more visionary kind. Talents for music, art, poetry, and mathematics do not contribute towards the preservation of the human species, and therefore they cannot have arisen by the operation of natural selection.

Perhaps, however, the development of the musical sense in man depends on sexual selection, as we have seen that it does in insects and birds. Darwin held this view; he supposed that the primitive song of man originated in courtship. I am doubtful whether this opinion can be sustained, but the point will be referred to further on. If, however, the theory be accepted, if we admit that sexual selection played a decisive part in the first development of human song, even then we have gained very little as an explanation of the origin of our own music, because sexual selection is insufficient to explain the immense growth which must have taken place in the musical sense since the earliest times, if we admit its existence in primitive man.

We might perhaps be inclined to maintain that such a growth of the musical sense has actually occurred, when, without referring to primitive man, we simply compare the

music of the savage with the highest achievements of our own art.

When Europeans first visited the islands of the Pacific, all the natives were found to practise some sort of music. The song of the New Zealanders made a profound impression upon Cook, and Chamisso found the song of the Hawaians and Tahitians extremely pleasant, although often accompanied by an orchestra of noisy instruments, such as drums, hollow tubes which were struck violently against the ground, and wooden sticks which were knocked together.

The 'music' was confined within the limits of a very few notes, lying between E and G (or, in the case of Tahiti, between C and F), although, at the same time, not only semitones but quarter-tones (or 'semi-semitones') were employed.

The song was pure, and when a hundred sang together, the sound was like that of a single voice. In spite of the limited compass of their scale, they had a rather large repertory of different melodies and themes, which however were always characterized by monotony and unceasing repetition : some of these were used as the accompaniment of work, others for rowing, dancing, marching to battle, and mourning the dead.

We must however remember that the Polynesians are not in a very low state of civilization. Their poetry is by itself sufficient to prove this, for it is full of feeling and abounds in beautiful similes. Hence we can scarcely look upon their music as primitive if this expression implies the lowest form of musical art.

And yet, what an enormous difference, when we compare this with one of the great musical works of our own time, such as Bach's Passion music in all its depth and magnificence, Mozart's G-minor Symphony, or one of the nine 'Revelations' (so to name them) of Beethoven. One would almost hesitate to apply the term 'music' to the primitive successions of notes made use of by 'savages,' so monstrous does the difference between the two entities appear. Yet our own music must have developed itself from similar beginnings,—there is no other way. And, in fact, we find similar elements in both; notes of definite pitch, separated by definite intervals and held for diverse lengths of time, that is to say, distinguished by differences of rhythm. So that, in this manner, we arrive

at the musical theme, the melody, the groundwork of all music.

Even in its savage form music becomes, to a certain extent, the expression of emotion. The funeral dirge is very different from the war-song or the festal song. Of course such melodies are very far from attaining the marvellous precision with which the highest music can not only excite the whole range of human feeling, but can also represent every emotion just as a drawing represents form. And music can achieve this with such fine shades of expression that language is by no means its equal.

Disregarding for the present those highly gifted minds that created such music, and only considering those which enjoy it, it is clear that even for the mere understanding, viz. the appreciative enjoyment, of one of our great performances, there is required a far higher musical sense than is necessary for the comprehension of the monotonous song of a negro tribe, or a simple Chinese melody, or one of those melodies in octaves which played so prominent a part with the ancient Greeks. In order to hear in a symphony of Beethoven or in Bach's Mass in B-minor anything more than a mere confusion of notes, or a roaring, heaving ocean of sound, demands a highly developed musical intelligence.

Considering these facts, the assumption seems at first almost unavoidable that musical talent in man has gradually increased from the condition found in the Polynesians up to the level reached by the most civilized nations; and if for the moment we adopt the Darwinian hypothesis as to the origin of human music, it is clear that the amount of increase which has taken place during this rise from the condition met with in the living savage ought to be sensibly greater than that which took place during the development of primitive man into the living savage. It is at any rate certain that the amount of increase in the musical art itself has been far greater during the second period of its development than it can have been during the first.

Hence we are led back to the question with which we started, viz. how and by what means can this increased refinement and growth of the musical talent have been produced?

Sexual selection cannot possibly afford the required explanation, even if we admit that it played a part in the origin of the primitive song of ancestral man. It is not only true to-day

but has been true from times immemorial, that the choice of husband and of wife are determined by qualities other than musical gifts, viz. by youth, beauty, strength, and not least by mental endowments, not to speak of the various external inducements which are always apt to intervene. No one will be prepared to maintain that men who cannot sing and lack any remarkable musical talent, are or ever were at a disadvantage in gaining wives. On the contrary, we know that such men have no difficulty in finding unmusical partners, and indeed that they not uncommonly marry those in whom this taste is strongly marked. If this be so any increase of the musical talent by means of sexual selection is rendered impossible.

I feel sure that many will at this point inquire whether it is impossible for musical talent to have grown in exact proportion to its exercise. We are all familiar with the fact that by constant practice every organ is improved and its power increased. We cannot doubt this when we think of the marvellous delicacy of touch acquired by the finger-tips of a blind man who attempts to make up for the loss of vision by means of the tactile sense. Why then should not the musical sense have been increased during the course of unnumbered generations in each one of which the mind and ear were exercised in the composition of music and in its enjoyment? And such exercise appears to have actually taken place, for, as far as we are aware, nearly all savage nations, not only the Polynesians, but the American Indians, negroes, and Asiatic tribes,—possess some sort of musical utterance.

This explanation would certainly be a very simple one, and it would be equally useful in many other directions, provided only that it were the true one. Up to the present time it has been regarded as valid, and many, even now, consider it to be so. But the explanation before us involves a supposition which a close examination does not allow us to admit,—the supposition that those modifications of an organ which are due to its exercise during the individual life can be transmitted to offspring. The supposed increase of the musical sense in the course of generations can only have occurred in the manner suggested, provided that this supposition be granted. If however the results of practice cannot be handed down it is clear that the increase of the sense starts in the descendant at the

very point at which it began in the parent, so that growth in the former can only reach as far as it did in the first ancestor, and this in spite of practice continued through any number of generations.

The amount of improvement possible in a life-time is very limited. No athlete can by any amount of practice lift a weight of a hundred or even one of twenty hundredweight, although he may be able to raise three or four. And, if our views on heredity be correct, the son of an athlete will have to start at the point at which his father started. For the son, if indeed he inherits his father's gifts, inherits only those with which his father came into the world and not any increase which they may have undergone during his lifetime. Unlimited training therefore will only enable the son to lift a weight of three or four hundredweight.

Biological science asserts, with ever increasing clearness, that there is absolutely no evidence for the assumption until recently so generally received, that acquired characters can be transmitted. It was believed that mutilations were occasionally inherited, but a searching examination has shown that the evidence brought forward will not stand the test of criticism. The results of certain recent experiments, in which the tails of mice were amputated, showed that the offspring, although examined in many hundreds of cases, were invariably normal [1].

We are therefore compelled to abandon this hypothesis of the transmission of acquired characters, at any rate until it has been supported in some other way. We lose with this view a very convenient principle of explanation, and we must therefore attempt to understand the phenomena without its aid.

The question before us is :—How is it possible that such an increase in the musical sense took place as seems necessary to have raised it from the condition met with in the savage up to that found among civilized races at the present day? When we examine this question we are led to inquire *whether it is correct to assume that any increase in musical talent has, as a matter of fact, taken place in the course of ages.* That such an increase has occurred appears to be a matter of course; for how could our highly developed music have arisen unless the musical organ had previously become more efficient?

[1] See Vol. I. pp. 444, 445.

Let us however consider the converse question:—*Is it the case that highly developed music must appear when high musical talent exists?* Let us suppose for instance that a child endowed with the talent of a Mozart were born among some savage nation such as the Samoans before they were influenced by European civilization. Would such a child, after reaching maturity, compose stringed quartettes and symphonies? Certainly not. If the Samoans possessed the songs which they have to-day, our aboriginal Mozart must soon have known them all by heart and would have composed new ones. Perhaps, being such a unique genius, he might have produced a great musical reform, introducing changes of a revolutionary character and raising Samoan music to a higher stage. But he would not have raised it to the modern symphony. In order to attain such a height he would have been obliged first to invent the musical notation, and then, rising higher, to pass through polyphonic music, until at last he reached the commencements of that harmonized music to which symphony belongs. The greatest change that he could have introduced would have been an extension of the scale from three or four whole tones to seven, and in association with this, the composition of more elaborately constructed melodies, or at the utmost the invention of music in two parts, which is known to have taken place comparatively recently, viz. in the times of the Troubadours.

It would have been as impossible for the Samoan Mozart to compose symphonies as for one of the great men of science of ancient Greece, such as Archimedes, to invent the modern dynamo as used for the transmission of energy or for electric lighting. To be enabled to construct such a machine, he would have had to work his way through more inventions and discoveries than could have been made during the life-time of the greatest genius who has ever lived. For in ancient times nothing was known of electricity except that amber (electron) when rubbed attracted little pieces of paper. Before a man could arrive at the knowledge by which he could construct a fixed electro-magnet in such a manner as to produce currents in a rotating coil, many other discoveries in physics had first to be made, the investigations of Gray, Dufay, Kleist, Franklin, and others were necessary, Galvani and Volta had to discover

the electric current, Oerstedt electro-magnetism, while it was necessary for Seebeck, Ampère, and Faraday to base upon this still further discoveries. In like manner most of these discoveries had to be made before first Soemmering and then Gauss and Weber could use the electric current for signalling at a distance; and even then a whole series of practical improvements in telegraphy necessarily preceded Hughes' printing telegraph. One discovery is ever built upon another; and the history of music is not less a history of inventions than that of the electric telegraph.

It is therefore impossible for even the greatest genius to pass directly from simple melody to symphony.

I should like to suggest the further question whether it is quite certain that Mozarts could not have existed in ancient times; in other words, whether the supposed increase in musical talent has in reality taken place as a historical fact, or whether the talent was not inherent in man from the beginning, while its expression, i. e. music itself, has undergone progressive increase and development.

At first sight the question may appear to be very strange; but I believe that it is perfectly justifiable. Indeed I am of the opinion that the suggestion implied in the question is entirely valid. I have shown that from the mere fact that symphonies are not composed by savages, we are not entitled to conclude that Mozarts have not existed among them; or, to put it still more clearly, we are not entitled without further proof to infer that savages never possess high musical talents because their music is but lowly developed. Such talent might very well exist, but could not produce any marked effect, because of the low level attained by the musical environment.

I am satisfied by the proof afforded by numerous facts that this is really the case, and that therefore the high musical talent which is more or less possessed by civilized man at the present time, does not depend upon a gradual increase in the musical sense, and that such increase being non-existent does not require explanation. No such rise and increase of the musical faculty by itself has taken place. The musical sense is rather an ancient possession of mankind chiefly depending upon the highly developed auditory organ, and this was transferred to man from his animal ancestors and has not

increased at any rate beyond the condition reached by the lowest of existing savages. We have definite proofs of the occurrence among savages of musical talent capable of the same education as our own. We must therefore consider their talent to be as high as ours, although it is generally hidden because untrained during the life-time of its possessor.

Negro races are certainly not at a very high stage of civilization. We see this clearly by their utter carelessness of human life, as shown in the dreadful massacres of the King of Dahomey and other chiefs, by the state of servitude to which women are subjected, and by the lack of real family life. But in spite of these proofs of inferiority it has happened on many occasions that negroes have attained to the full understanding of our highest music.

Brindis y Salas, a Cuban negro, who travelled as a violinist through Europe and America, is a well-known proof of this. He was not merely endowed with excellence of 'technique' along with delicacy of ear, but—as I am told by a distinguished musician[1]—'he possessed musical abilities of a very high order. His playing was that of an artist.' He must therefore have had an inborn musical sense, as high in all essentials as that of our greatest performers. It is impossible to urge the objection that his ancestors had been under European influence for centuries, because such a period of time would be far too short for the growth of a special part of the brain as the result of inherited practice, and also because European music of a high order does not reach the negroes of Cuba.

Another example is afforded by the 'Jubilee Singers,' a company of negro men and women, who in 1887 astonished Europe by their 'very extraordinary performances in four-part singing.' The authority, whose opinion I have already quoted, judges from their performances that there is no doubt whatever as to 'the talent of the negro nation for our music.'

We also find among European musicians and composers many grounds for the belief that musical talent has not been increased by practice in the course of civizilation. If this were the case, highly gifted musicians would never have arisen in families living, remote from the great influences of their

[1] This information was kindly placed at my disposal by Herr Otto Lessmann, of Berlin, editor of the 'Allgemeine Musikzeitung.'

time, in places where the only music consisted of national songs accompanied by the guitar or the zither. But, not uncommonly, from these very surroundings have come men with a highly developed musical sense, and even celebrated composers. Martin Luther, who is known to have been a composer, was the son of a poor miner. Palestrina was the son of a peasant. Jacob Callwitz, a sixteenth century composer, was the son of a labourer, and Joseph Fux, who composed in the seventeenth century, was the son of a Styrian peasant. Cimarosa was the son of a washerwoman near Naples: John Gottlieb Naumann, a renowned composer of the eighteenth century, was of peasant extraction, as also was Joachim Quanz. The first known ancestor of the Bach family was born in 1550, in the country near Gotha, and worked all his life as a miller in Wechmar, his native place. Joseph Haydn was also born in a village, and was the son of a poor wheelwright.

In these instances we cannot maintain that all this musical genius sprang out of the earth suddenly and without preparation. On the contrary, I wish to point, for example, to Haydn, whose parents we certainly know to have been musical. They sang when they rested from work, and the father accompanied on the harp. The above-mentioned founder of the Bachs also frequently played on the cythringen, a kind of guitar, which he brought home to the mill from his travels. Sebastian Bach says that 'this was, as it were, the beginning of the music of his descendants.' The highest musical culture of their time was entirely without influence on the musical sense of the ancestors of these two great musicians; the talent existed nevertheless, and appeared in the descendants, sometimes to an increased and sometimes to a diminished extent.

It is no real objection to this argument to urge that only a few out of the large number of musicians in recent centuries came from the lower orders. A great musician not only needs the highest talent, but also stimulus and all the culture that his times can bestow. I previously assumed that the invention of two-part singing would be the highest achievement possible for our supposed Samoan Mozart, and we may safely conclude that Joseph Haydn would never have surpassed his father's national songs and harp had he not chanced to become

a chorister in the little town of Hainburg, and had he not afterwards entered the music-school in Vienna, of which Reutter, the organist of the cathedral, was the head. Haydn possessed musical talent of the highest order, but had it not been trained, he could never have accomplished by himself the whole development of modern music from the national song; he could never have risen from the music of his parents to oratorios and stringed quartettes. Such cases afford interesting evidence that at least a great part of the development of modern music can be accomplished in a lifetime, even when all the ancestors have been strangers to the higher musical culture, so that it was impossible for their musical sense to be raised by it. The musical sense is evidently innate in the human brain, and is independent of all training and practice undergone by ancestors. The predisposition may be strong or feeble, but even the greatest talent does not enable the possessor to climb to the height reached by the music of his time without being raised by instruction. That so great a height can be reached in a life-time by the son of a German peasant, or even by the offspring of a savage race, evidently proves that the musical sense of to-day has been inherent in man since times immemorial, and that it has not been increased by the development of music or by practice. It has nevertheless been brought to a higher stage of development in the most civilized races, as we shall see further on.

We have already seen that musical talent exists in every stratum of society. And yet the upper classes have produced many more eminent musicians than the lower, a fact which we can easily understand when we remember that without early stimulus, and the constant opportunity of hearing and being instructed in the highest music, even the greatest genius must remain undeveloped or, as we may say, latent.

This is proved by many examples: thus out of sixteen renowned German musicians of the sixteenth and seventeenth centuries, no fewer than eight were the sons of organists: the others were the sons of peasants and labourers, but nearly all were choristers when boys. Furthermore, twenty-seven of the greatest German and Italian composers of the eighteenth and nineteenth centuries were the sons of musicians. Examples of these are afforded by Mozart, Beethoven, Weber,

Hummel, Cramer, Abt Vogler, Hasse, Johannes Brahms, Robert Volkmann, Czerny, Karl Reinecke, Cherubini, Bellini, Rossini, Antonio Lotti, and Scarlatti. In all these cases it is clear that a highly-developed musical sense was transmitted from father to son, while the talent of the latter was further developed than that of the father, because it was trained and exercised from earliest youth, although I do not mean to imply that it was not also greater from the very beginning. But the greater force of the inherited talent does not depend upon the weaker talent of the father having been improved by practice during his life-time. Many still believe in the hereditary transmission of improvement acquired by practice; but if such inheritance could take place so rapidly, in a single generation, we should easily find proofs of it in many occupations and pursuits—proofs which are as yet entirely wanting.

I shall, however, be asked: Whence came the increase in the talent of Mozart and Beethoven as contrasted with that of their fathers? It is impossible to give any definite answer to this question, but I can, perhaps, indicate it by another question: Whence came the high poetic genius of Goethe, whose father had no taste for poetry, while his mother without ever having written, exhibited, in her whole character, the most distinct endowments in this direction? How could the poetic genius of the mother, which had never been exercised, attain so high a level in the son? We must not forget that poetic talent is by no means a simple power but a very complex one, depending on a happy combination of many intellectual and emotional gifts, which in Goethe's case were derived, as he himself tells us, partly from the father and partly from the mother.

'Vom Vater hab' ich die Statur,
Des Lebens ernstes Führen;
Vom Mütterchen die Frohnatur,
Die Lust zum Fabuliren,' &c.

Similarly, I should be inclined to explain the genius of Mozart as a very complex power made up of the fine ear, the strength of will and energy of his father, and the bright and cheerful disposition, the gentleness and refinement of feeling of his mother. From this constitution may have arisen the infinite flexibility of that wonderful mind which, with unwearied

activity, ever led to fresh combinations of the emotions which became the subjects of musical themes. A psychologist might be able to show us more of the constitution of this marvellous mind. I will not attempt it; I merely wish to show that the increase in the musical faculty, which appears to pass from father to son, can be explained, as in so many other cases, entirely without the unproved assumption of the inherited effects of practice. Even when the musical sense itself is transmitted unaltered, viz. without increase, from father to son, a considerable increase in the power of composition may nevertheless be brought about by the combination of mental gifts derived from the mother with the musical sense inherited from the father; and this sense will therefore gain in the son a higher expression. There are many highly-gifted people who are unable to compose anything original: even remarkable musical talent may co-exist with an utter inability to produce anything new. Examples of this are perfectly familiar. But in the descendant of such person, the strong receptive musical talent may be united to such a complete flexibility of the mind and temperament, derived from the mother, that new combinations of ideas will ever arise. This latter gift will then seize upon the musical sense, and ideas which were perhaps of an entirely different nature in the mother, will become musical ideas in the son.

The composer not only needs the musical faculty, the gift of originality is also indispensable. I believe that an increase in the genius for music which passes from father to son depends upon a new combination of mental gifts, with which of course an increase in the delicacy of the musical ear itself may be united; for every inherited quality varies, and may be feebler or stronger than it was in the parent.

Let us now return to the argument that some external stimulus is necessary for the development of an existing musical faculty. Two facts seem to me to favour this opinion; first, that nearly all the renowned composers and singers of the present century have come from large towns, and have thus been brought up where from earliest youth they have been subject to musical influences of all kinds. I have made a list of ninety-eight such cases. Secondly, the fact that during the nineteenth century the Jewish race first began to take part in

the development of music. In this century composers of Jewish descent first begin to appear, and among them we find very great names, such as Meyerbeer, Mendelssohn, Halévy, Rubinstein, Moscheles, Félicien David, and others. This fact is probably associated with the emancipation of the Jews, which afforded them the opportunity of developing the rich musical faculty which they possessed by nature. In this we find a further proof that it is impossible for the musical sense of modern nations to have been raised by practice during earlier centuries; for the Jews were entirely without adequate musical training, so long as all the higher music was bound up with religious service. The introduction of music into the Jewish synagogue is of quite modern date. Throughout the eighteen centuries preceding our own, music had played no part in Jewish life, and yet this nation possessed the musical faculty in a very high degree, and as soon as the Jews began to cultivate their talent they were not only able to reach the summit of modern musical achievement, but also to contribute towards the progress of the art. This is certainly clear evidence for the hypothesis that the musical faculty has been latent in mankind from times immemorial, at least in many races, and that it can be evoked at any time and raised to any height.

But if the mental instrument with which we make—I mean invent and enjoy—music, existed at all times, why did not man perform symphonies and oratorios in the age of the Pharaohs? The answer is clear—*Because music is an invention*, and one which could reach its present height only very slowly in the course of centuries. And here we meet with the great difference between man and animals. Man possesses a *tradition*; he improves and perfects his performances by passing on the gains of each generation to those which follow. The higher animals are not entirely devoid of the power of learning from preceding generations, but they possess it in a much lower degree. A young goldfinch, when brought up by hand, sings untaught the song of its kind, but not so perfectly as when it has had an accomplished songster for its teacher. It also learns by tradition, but the essential basis of the song was present in its organization beforehand, and is inherent. The bird speaks, even when untaught, the language of its species.

Sexual selection, as we may suppose, has made this language an essential part of its being.

It is otherwise with man: his language does not exist as a perfected faculty, as a part of his physical nature; but only as a possible expression of it which only becomes actual when the individual preserves communication with those who preceded him, viz. when he is taught to speak. Hence it is that every human child can learn any language: hence it is that there is not one single human language but hundreds of them, each of which has had its own developmental history—its origin, climax, and decline. Each of these different modes of expression of the human mind seems, as it were, a distinct mental entity, independent of the individual, and possessing its own history. And this is not only true of language, but also of the arts and sciences. Not one of these could have existed had not man possessed that advantage over animals which enables him to transmit the knowledge he has gained to his descendants, so that these latter are benefited by building, from the very first, upon the high level reached by previous generations, from which they can rise still higher.

All this is far from new: it has long been known that the chief difference between man and animals consists in the fact that man is capable of mental development while animals are not. But I doubt whether the exact difference has ever been clearly conceived. The statement just made is not a satisfactory expression of it; for common knowledge of the day asserts that animals are certainly capable of development although in a sense entirely different from that which is intended above. We have every reason for the belief that the unceasing transformation of species which took place during the earlier epochs of the world's history, is also proceeding to-day—that to-day, wherever circumstances are favourable, the transformation of species is taking place, although slowly and insensibly. But such a process of development of one species of animal into a new one, even when combined with an improvement and increase in efficiency, is entirely different from what we mean by the development of mankind.

The development of animals transforms one species into another and changes the physical nature: but what we generally understand by the intellectual development of man-

kind by no means necessarily entails any physical alteration even in the brain itself: it is indeed quite independent of any such change. Such development represents *an increase in the intellectual acquirements of mankind as a whole*: this is the origin of civilization, using the term in its widest sense and applying it to all the numberless directions taken by civilizing forces[1]. Man, availing himself of tradition, is able, in every part of the intellectual domain, to seize upon the acquirements of his ancestors at the point where they left them, and to pursue them further, finally himself leaving the results of his own experience and the knowledge acquired during his lifetime to his descendants, that they may carry on the same process. This method of progress is most clearly shown in the history of science, and especially in that of natural science, which deals with an immense number of facts and experiences which have been very slowly acquired, collected, and transmitted to descendants during many centuries of civilization; and in this way alone could the present state of our knowledge have been reached. The human being of to-day can be easily raised, by a short period of training, to this stage from which, if he be successful, he may perhaps make one or more onward steps.

This consideration affords especially clear evidence for the assertion upon which I have already laid great emphasis—*that the development of any mental faculty is not necessarily connected with any elevation of the mental capacity of the individual.* Hardly any greater power of observation or more acuteness is required to observe the development of an Infusorian under the microscope, than was needed in Aristotle's time to make out the anatomy of a Cuttlefish, with the naked eye and simple

[1] Very similar ideas have been recently expressed by D. G. Ritchie in his '*Darwinism and Politics*' (London: 1891). Thus on pp. 100, 101 he writes as follows. 'Language renders possible the transmission of experience irrespective of transmission by heredity. By means of language and of social institutions we inherit the acquired experience, not of our ancestors only, but of other races in the same sense of "inheritance" in which we talk of people inheriting land or furniture or railway shares. Language renders possible an accumulation of experience, a storing-up of achievements, which makes advance rapid and secure among human beings in a way impossible among the lower animals. Indeed, might we not define civilisation in general as the sum of those contrivances which enable human beings to advance independently of heredity?'—E. B. P.

dissecting instruments. The fact that we can now solve more difficult problems than at the beginning of this century, or in Aristotle's day, does not depend upon any increase in the capacity of the human brain or any improvement in the delicacy of the faculty of observation; but it depends upon the heritage which we have received from our ancestors, viz. higher problems left for our solution together with better means and appliances for their investigation. *It is as impossible to explain the development of music by an increase and perfecting of the musical talent, as to explain the superiority of our pianists over those of Mozart's time by a recent improvement in the dexterity of the human hand.* The very hands which, in Bach's day, could only give a bald and imperfect performance on the spinet, would now, upon a Steinway's or Bechstein's grand piano, produce all the enchanting effect of an orchestra. The causes of this immense change are manifold. First, a gradual improvement in the instrument,—itself a result of tradition which permitted an advance upon the acquirements of earlier generations; secondly, parallel with this advance, the development of appropriate music; lastly, the immense improvement in pianoforte technique which we associate with the names of Haydn, Mozart, Clementi, Hummel, Moscheles, Thalberg, and Liszt. No one would dream of suggesting that this advance in 'technique' is due to an improvement, as regards piano-playing, in the powers of the human hand, produced by the practice of several consecutive generations. Such an origin is indeed impossible, because, happily, every one does not play the piano, because every pianist is not a performer of eminence, and because the children of such performers rarely become performers themselves. Liszt's father was a clerk in an accountant's office. Among all our living performers I only know one, Pauer of London, whose son is a pianist. It is clear that in this case also the possibility of higher performance does not depend on higher talent, but upon the tradition of improved technique which enables the young artist to strive, from the very first, after a higher ideal.

It is the same, I believe, with music itself—nay with all the arts. That emotional instrument wherewith we make music, whether developed within us or received from without, has been innate in man, and has undergone hardly any

improvement from times immemorial. But in these days we know how to employ it more fully because we have trained it to higher achievement from the very beginning of life. The musical talent, like every other, is capable of vast improvement by life-long training. I well remember hearing for the first time, as a boy of thirteen, a great performance—the Pastoral Symphony of Beethoven. How clear and distinct is the meaning of such a composition now that we are accustomed to hear far more intricately written orchestral works! I was even then impressed by the mighty ocean of music, and listened with the greatest interest; but I was unable to disentangle the theme from the maze of notes and to understand its ideas. It was only by practice of my mental sense, through frequently listening to this symphony, that my power of musical perception acquired the capacity of picking out, and distinguishing, particular passages more and more clearly from the totality of the composition, and placing those passages into their due relation to the swell of the waves of music which surged along beside them.

Although the average musical faculty has not undergone any increase, in the course of ages, it must at one time have originated; and the question arises whether we can explain this from a scientific standpoint. *How can we conceive the existence of a musical sense?*

Attempts in this direction have been repeatedly made, not only since the doctrine of evolution has become prevalent, but also during past centuries. The able psychologist C. Stumpf has recently directed attention to the fact that the question of the origin of music greatly occupied men's minds, especially in France, during the middle of the last century. Jean Jacques Rousseau had already formed the opinion that music originated in language, in excited speech, a view that was simultaneously brought forward in Germany by Scheibe. This hypothesis must have been forgotten later on, or Herbert Spencer would never have enunciated and supported it without reference to his predecessors. It has met with little acceptance, and has been refuted in detail; it may now be looked upon as an abandoned position. This can hardly be said of the hypothesis brought forward by Darwin, who held the antagonistic view that song is older than language, and arose by sexual selection.

Important objections have however been raised against this hypothesis by many writers, and especially by Stumpf. And yet I would freely admit that at present it is difficult, nay impossible, to decide whether sexual selection has or has not had any part in the origin of human song. But even if it has played this part, it by no means follows that there was a similar origin for the musical sense also: this faculty might have been present beforehand.

It would lead me too far if I were to attempt any detailed exposition of the reasons which, as I think, oppose the hypothesis of the origin of the musical sense by sexual selection. They partly depend upon the above-mentioned fact that any increase in this faculty has not taken place since the stage reached by man in a savage state. Other objections depend upon certain considerations of which I will now speak. The explanation of the musical sense is to be looked for in an entirely different direction; I do not believe that it originated as something independent and as it were intended for the duty it performs, but that it is simply a bye-product or accessory of the auditory organ. This organ was a necessity in the struggle for existence and has therefore been developed by selective processes, and raised to the highest pitch of perfection. The musical sense is, I believe, a merely incidental production and thus in a certain sense, an unintended one.

No one can believe that the human hand was created for playing on the piano,—that it became what it now is in order that man might be able to make use of this instrument. It is, as we know, fitted for grasping and for the power of delicate touch; and as these are very useful qualities, of high importance in the struggle for life, we feel no difficulty in explaining the gradual perfecting, by processes of selection, of that form of hand which the higher animals had already gained. By means of selection, the hand became the perfectly articulated, sensitive, and mobile structure that we find, not only in ourselves, but in the very lowest savages. But we can do many things with our fingers which were never intended, if I may use the expression; we can, for instance, play on the piano, now that this instrument has been invented. And furthermore a native African could, if trained as a child and under certain conditions, learn all the technique of the modern piano as thoroughly as a European.

I believe it to be much the same with the musical sense and the artistic faculty in general. This faculty is, as it were, the mental hand with which we play on our emotional nature,— a hand not shaped for this purpose, not due to the necessity for the enjoyment of music, but owing its origin to entirely different requirements.

I will give more detailed evidence in support of this view. Our musical organization consists of two parts :—first, the auditory organ proper, viz. the outer, middle, and inner ear, by which the various sounds become nervous stimuli, each producing its corresponding nerve-impulse : secondly, that part of the brain which transforms the impulses conveyed to it by the auditory nerve into sensations of sound ; this is the auditory centre of our brain.

The first part of this twofold organ, the auditory organ proper, is, so far as we know, not much higher in organization than that of many animals, and it does not possess any peculiarity of construction which would justify us in the assumption that the power of *hearing* music is greater than in animals. The higher animals can certainly hear music : the behaviour of my cat is sufficient evidence for this, for she comes near whenever the piano is played and sits quietly near the performer, sometimes jumping up into his lap or even upon the keyboard of the instrument. I know of a dog, kept by a family in Berlin, which always approached when music was played, often coming from distant rooms and opening the doors with his paw. I hear, on good authority, of a dog which generally stayed at home, but wandered about every now and then in order to indulge his love of music. This dog could never be kept at home during the fair which is held twice a year at Frankfort-on-the-Main. As soon as the street bands appeared and began to play the dog ran off and followed them through the streets of Frankfort from morning till night. This habit was well known by his owners who were accustomed to keep dinner for him in the evening at the time of the fair.

It is sufficiently clear that neither cats nor dogs nor any of the other animals which hear the music of man were formed with a view to the perception of such sounds. I mean that the auditory organ which they possess, arising under the guidance of natural selection, *cannot have assumed its present form in*

order that these animals might perceive music; for such an experience confers absolutely no advantage in the struggle for existence. Besides, the animals and their auditory organs are far older than man and his music. The faculty of hearing music possessed by these animals must be an incidental accessory power possessed by an auditory apparatus which assumed its present form under the operation of other causes.

Now I believe that it is the same with man. Man, too, did not acquire his power of hearing music as something by itself, but he received, by processes of selection, a very delicate and highly elaborate auditory organ; for this organ has been necessary in the struggle. And furthermore, it so happens that this organ can also be used for hearing music. By the assertion that the auditory organ of man was produced by natural selection, I do not mean to imply that it was not already formed in the pre-human period. We have never found the direct ancestors of man, and even if we were fortunate enough to meet with their remains it would be impossible to make out the minute microscopic structure of the soft tissues which, during life, covered the osseous parts of the auditory apparatus deeply buried in one of the bones of the skull. But it is most probable that our direct ancestors possessed an auditory organ nearly similar to that which we possess to-day; for in the living caricatures of men, the apes, it reaches almost the same degree of perfection. It must be admitted that there are no researches into the minute details of the ape's ear like those of Hasse and Retzius on the auditory organ of certain other Mammalia. Hence we cannot decide whether the length of the scale which can be heard by an ape is as great as that heard by a man; but we may assume that it is nearly the same.

The power of appreciating the interval between musical notes depends, as we know, upon a wonderfully complex apparatus placed in the so-called cochlea. This structure called after its discoverer, Corti's Organ, consists of thousands of cells which form the terminations of auditory nerve-fibres: each cell can only be made to vibrate by a single note of a certain pitch. This is brought about by the fact that each cell rests upon part of an elastic membrane of microscopic delicacy which passes across the cavity of the cochlea, just as upon a stretched string which only vibrates with a particular note. If Helmholtz's in-

terpretation of the apparatus be correct, we can judge of the delicacy of any auditory apparatus by the number of such cells. The greater the number of cells the more delicate will be the hearing of the animal and the wider will be its range. The exact measurement and enumeration of Retzius have shown us that the human cochlea contains 15,500 such cells, that of the cat 12,500, that of the rabbit 7,800. Hence man has a more perfect sense of hearing than either of these two animals, but we cannot determine with certainty whether he can better appreciate minute differences, or whether he can hear more notes: probably he is superior in both these respects. There are also individual differences in the number of cells in the human species, although perhaps only within narrow limits. Such differences explain why some individuals do not hear so well, or cannot distinguish so many deep or high notes, as others. I myself possess a rather fine ear, but I can never hear the high notes of certain species of grasshoppers, even when hundreds of them chirp together, although others can hear them easily.

If then the apparatus by which music is heard in the cat and the rabbit be essentially the same as that of man, only differing in degree, the following question is naturally suggested:—*Knowing that nothing can arise unless it be useful, how has it been possible for this apparatus to originate?* The power of hearing music must have been utterly useless to those animals which do not make music, and hence the origin of their auditory apparatus must have proceeded from other necessities. What can these necessities be?

Why has it been useful to Mammalia in the struggle for existence to hear with distinctness all the large number of notes for which their auditory apparatus is fitted, and which renders the hearing of music a possibility? This question has probably never been asked before, and I must admit that the answer is by no means easy; at any rate if a complete and detailed explanation be expected. But I believe that it is easy to understand in a general way how the ear of these animals could have been elaborated and raised to so high a pitch by natural selection. Wild animals stand in need of a very fine ear. Beasts of prey, such as cats, must in the first place be able to hear and distinguish between all the sounds made by

their prey. But this means that they must hear a scale of considerable length; that, for instance, of the cat must pass through all the interval between the cooing of the wood-pigeon the call of the cuckoo, and the notes produced by the blackbird, the chaffinch, the linnet, the siskin, the thrush, and the pheasant. But the wild animal must also be able to hear the sounds made by its enemies and distinguish them from others. And not only is this the case with the animal sought after by many enemies, such as the rabbit, but the enemy itself must also be upon its guard against other enemies which endanger its life and that of its young. It must distinguish the howl of the hungry wolf from the bark of the fox or dog, the deep note of the eagle owl from the cry of the eagle and vulture. We need not here take man into account, because his existence only began long after the development of the auditory organ in these animals, and because his influence upon them has been annihilating rather than transforming.

It was therefore necessary for the auditory organs of these animals to have a very extensive range, stretching from rather low notes on the one side to very high ones on the other. It was essential that the organ should be adapted for a continuous scale without breaks; for otherwise the position of the various notes could not have been accurately estimated. Indeed we feel a sense of admiration and wonder when we see the exceedingly high development of the cochlea adapted for hearing a continuous scale in the mammalian ear, and we can only understand it when we realize how completely the very existence of wild animals depends on the utmost delicacy of their organs of special sense. It is absolutely essential for them to know with certainty whether any particular sound proceeds from an enemy or from their prey. While a single mistake might be fatal to them, one often repeated would be inevitably punished with death. If they mistook the sound made by an enemy for that of their prey they would of course go to certain destruction, but the opposite mistake would also be fatal; for the food of a beast of prey is nearly always scarce, and if many opportunities were missed the animal would die of starvation. It is not in vain that the fox roves about by night and day searching for food, listening for the faintest sound, and ever ready to rush upon its prey or to fly; it is not in vain that the hare is so

timid; it needs to be extremely sensitive to every sound if it is to continue to exist as a species. Hence we can perhaps to some extent understand why the rabbit has 7800 cells in its auditory organ, although this implies the most astonishing delicacy of ear. We must not however assume that each of these cells is set to a different note, but rather that the four cells of each transverse row are fitted to receive the same vibration. There remains, however, a surprisingly large number of different note-sensations, i.e. nearly 2000. We can realize how very delicate hearing must be, which can appreciate only 1000 different notes, when we remember that a concert grand piano contains only 87 different notes. If we reckon that the auditory organ can appreciate a somewhat longer scale, namely that of a hundred notes situated at the distance of semitones, it follows that the interval between two consecutive semitones would contain nearly 19 intermediate sounds. The human ear, when very highly trained, can distinguish nearly 30 intermediate notes between A and B-flat, a rather larger number than the difference between the numbers of their respective vibrations in a second,—(A = 440, B-flat = 467·5).

If then the mammalian auditory organ must attain so high a pitch of perfection lest it should be inadequate in the struggle for life, it is clear that the part of the brain by which notes are perceived, the auditory centre, must possess a corresponding degree of organization. We may indeed assume it to be certain that a corresponding degree of development is found in those layers of nerve-cells and nerve-fibres in the auditory centre, the so-called 'field of memory,' which serve as the material basis of the memory of auditory perceptions. Aristotle was quite correct in maintaining that 'animals devoid of memory would be unable to perceive even the difference between two successive notes[1].' But an elaborate auditory organ would be of little or no value to such animals; they would be unable to discriminate between the sound of an enemy and that of their prey, for they could not compare the note they were hearing with that previously heard, the latter having wholly faded from their consciousness.

It is much to be regretted that we can know with certainty in but few cases how far an animal is capable of perceiving

[1] I quote from C. Stumpf, 'Tonpsychologie,' Bd. i, p. 279.

music. The capacity seems to be present in a tolerably high degree; for it is known that cavalry horses often recognize the signals as well as their riders and begin the appropriate movements before being directed.

The evidence is especially clear in the case of certain birds, far below the above mentioned mammals in mental power, that music may be heard and properly understood by organisms which cannot have acquired their auditory apparatus for this purpose. I am here referring to those birds which either have no song of their own or a very simple one, but which are nevertheless capable of imitating the more beautiful song of other birds or even the melodies of human music.

This is especially remarkable in the case of parrots, which can learn to sing short melodies quite correctly. It is therefore certain that they possess the apparatus necessary for hearing music, although they do not sing unless taught.

Hence the supposition appears to be well founded that man possessed the auditory apparatus necessary for music before he made music, and that the apparatus did not, by making music, attain the degree of development it has reached. It is not necessary to assume that the capacity of hearing music was a primitive faculty acquired for its own sake; it may rather be conceived of as a secondary, an 'unintended,' accessory, as a mere incident in the evolution of the auditory organ which reached its high development by ministering to other necessities.

It might perhaps be objected that neither the minute structure of the cochlea nor the power of hearing an extensive scale proves that music is perceived as music, or that we do as a matter of fact hear the third or fifth which is sounded. It might be conceived that the musical sense depends upon yet another and unknown peculiarity of the auditory apparatus, a peculiarity which has been added to the function of hearing and the origin of which therefore demands some special explanation. But this objection will not hold, because animals such as the horse and parrot, can as a matter of fact hear music, although we cannot assume that they possess any special contrivance for it. The basis on which this objection rests is nevertheless sound, for we can never explain the faculty of hearing music by the knowledge of our auditory apparatus alone. But to use this

undoubted fact as an argument for the conclusion stated above, would be like maintaining that the hand was specially created in order to play the piano, because we can never explain, by a mere examination of its structure, the infinitely rapid movements made by a performer. It might be argued that inasmuch as the hand and fingers were never required to make such swift movements when man existed in a primitive state, they could not have been originally capable of such movements, and that therefore the faculty which they now possess must have depended upon sexual selection or the results of inherited practice.

The same might be said with regard to the swift movements of the fingers in writing. Such arguments depend upon a mistaken application of the principles of utility, a principle which certainly excludes the possibility of raising an organ by the process of selection above the highest point of actual utility, but which by no means prevents it from acquiring new uses as the result of life-long practice.

A more serious objection may be derived from the consideration of those who are utterly unmusical. We cannot doubt that many such people exist, even if most of them are to be accounted for by want of training at the right time. Those who are totally devoid of the faculty of music, can apparently hear sounds and notes of every kind as fully as musical people, but they are unable to discern the intervals, or to perceive and reproduce a melody, much less to analyse a harmony. If then their auditory organ be normally developed we are apparently confronted with the proof that musical hearing is different from ordinary hearing, and has been superadded to the latter,—that therefore it cannot be merely an inevitable accessory, but has sprung from a source which demands some special explanation.

This argument appears to be sound, but I do not believe that it is so. The assumption that the hearing of unmusical people is as highly developed as that of the musical is utterly unproved, and I believe that it is most improbable. It is to be regretted that there are no sufficiently exact researches into the ordinary hearing of unmusical persons, and that we have even less knowledge of the minute structure of their auditory apparatus. But from what we know of musical hearing it follows that the

ordinary hearing of such people must be imperfect and their auditory apparatus abnormal in structure.

The meaning of the word 'unmusical' is merely relative. Mozart possessed such a wonderful memory for absolute pitch that he once remarked, directly he began to play his own violin, that it was tuned half of a quarter-tone higher than one he had played two days before. But many people, although admitted to be very musical, have the feeblest memory, or almost none at all, for absolute pitch. They cannot tell whether the performance they are listening to is in the key of A, C, or F: their memory deals with intervals alone, and they are satisfied if only the relations of the notes in any piece of music are correct. This is certainly often due to want of practice, and it is also connected with the important part played by the pianoforte in the musical education of mankind. The note A is much more firmly fixed in the mind of a violinist and has a far more individual character for him than any particular note of the pianoforte scale has for the pianist. But it is equally certain that there are also differences of talent as regards the memory for absolute pitch. Leaving the greatest heights of musical genius, we find that the perception of intervals may also be deficient, and that such deficiency increases gradually in different individuals until we reach a case like that described by Grant Allen in which the notes sounded by two successive keys on the piano seem to be absolutely the same. Such defects in hearing can only be explained by some imperfection in the structure of the auditory organ, in this case in the organ of Corti. Hence such an auditory organ would not represent what we may suppose to have been the primitive ear of man before he began to be musical; it is merely an example of degeneration. A perfectly normal auditory organ must always be musical, and this not only with regard to the perception of intervals, but also to the recognition of absolute pitch. For even animals must possess the power of distinguishing a note as higher or lower than some other note of which the pitch is retained in their memory, and if they were incapable of this they would be exposed to countless dangerous mistakes. We certainly cannot regard the ear of Mozart as the primitive normal ear of mankind; we must rather regard it as an abnormality as much above the average as the ear of a moderately unmusical person is below it. But even Grant

Allen's extreme case proves that the perception of absolute pitch is retained by civilized man; for this individual distinguished high and low notes, although he could not perceive any difference between the successive notes of the scale when he played it.

Hence the different degrees of imperfection in the musical faculty seem to me to be traceable to defects in the structure of the auditory organ, to a more or less complete degeneration from its original and normal state. Defect and degeneration are, as everyone knows, apt to occur in any part of the body, and should occasion the least surprise in an organ which, like the human ear, no longer plays a decisive part in the preservation of the species,—a part which it must certainly have played ages ago when man lived under more natural conditions. In such times he needed a perfect ear just as wild animals need it now. The civilized man of the present day no longer depends on the acuteness and perfection of this sense; it is, to a certain extent, of no importance whether he has or has not the full number of 15,500 cells in his cochlea. But those persons in whom the number or perhaps the minute structure of these cells is below the average, or in whom the tension of the membranes is abnormal, will probably be unable to perceive musical intervals correctly or may be unable to perceive them at all; such persons are unmusical.

I do not mean this statement to imply that defects in Corti's organ are the only cause of a deficient musical faculty. In some cases perhaps the cause may lie in the auditory centre, viz. the part of the brain where the impulses of nerves, produced by the stimuli of sound-waves, are transformed into the perceptions which we call notes. Certain kinds of deficieney in the faculty even suggest that the auditory organ and centre may be quite normal, but that there is merely a less perfect and less complex interconnection between this and the other brain-centres, so that the mental perception of music is not possible although the music itself is correctly heard. It is especially interesting to compare such cases with the remarkable and extremely variable phenomena witnessed in those who, from the lesion of a small part of the brain, have lost, either wholly or in part, the faculty of perceiving and producing music, such loss being frequently associated with defects of speech. In addition to

Kussmaul's admirably explained observations, Kast, Knoblauch, and Oppenheim, among German pathologists, have offered interesting contributions to this difficult and complex subject, into which of course I cannot enter upon the present occasion.

For the present purpose I merely wish to show that deficiency in the musical faculty must always depend upon defect in the anatomical structure of the auditory apparatus, the auditory centre, or their means of connection. If this be so, the existence of unmusical people constitutes no objection to the view I have propounded as to the origin of the musical sense.

But must we really admit that the musical talent of primitive man was the same as our own? Can it be conceived that, in these remote times, there were born men who, educated in one of our schools of music, would have produced a Haydn, a Mozart, or Beethoven, or even an ordinary musician of to-day?

I am quite sure that this admission will never be made. For it is clear that the understanding of our highest music not only needs the auditory apparatus and auditory centre, together with the life-long training of these: something besides is absolutely indispensable, *a mind that is sensitive, impressionable, and highly developed.*

I will enter rather more fully into this point. The frequently mentioned auditory centre is not a mere supposition; it is known with tolerable certainty. When a certain part of the temporal lobe of the cerebrum is destroyed in a dog or monkey, deafness ensues, although the auditory apparatus remains uninjured. Such animals do not suffer greatly in health; they continue to live, but remain permanently deaf. And all the while the sound-waves are still converted into nerve-impulses by the auditory apparatus, and the impulses corresponding to the several notes are still conveyed to the brain by the fibres of the auditory nerve. But in the brain that organ is wanting by which these impulses are transformed into sensations and are brought into relation with consciousness; the animal is 'psychically deaf,' as the technical expression goes.

If on the other hand we were able to remove every part of the cerebrum except the auditory centre, then the mechanical conditions necessary for the production of sound-sensations would still remain, but the animal or the man would neverthe-

less be unable to hear, because nothing capable of becoming conscious of sound-sensations would be left in the brain. In removing nearly the whole cerebrum the mind would be lost together with all its accessory powers, thought, imagination, will, and self-consciousness. The 'soul' would be wanting, and hence even the most beautiful of the sound-sensations produced in the auditory centre could not be perceived because there would be nothing capable of perception.

I have only mentioned this hypothetical case in order to show that the way in which music is perceived depends not only upon the auditory centre, but quite as fully upon the organ which lies behind, receives the sound-pictures, and allows them to have their full effect upon it. If, as in the case supposed above, there be no mind, then not a single sound-image can be perceived; but with a highly developed human mind of infinite freedom and flexibility and rich in ideas, the 'parts' of a polyphonic composition which run through each other, and proceed by contrary movement, can be perceived as the most charming musical architecture; they make up an artistic structure of rich form, the several parts of which exhibit the most significant relationship, rising from and returning into each other, and ever presenting in each of its separate parts fresh features and new and interesting combinations. But the case is very different with the comparatively lowly organized brain of an animal such as a parrot; for the power of mind is insufficient to take in such an elaborate sound-picture, and the animal can only perceive a confusion of notes, although perhaps a pleasing one. Even after constant practice the parrot would be unable to follow the movements of the 'parts' of the composition, because it lacks the necessary intelligence. We know by its whistling that it can hear music, but even in this it makes but little progress, and can only repeat short pieces, because it does not understand the connection between the parts. There is of course a very marked difference between the musical perception of a parrot's brain and that of a man. But a comparison between the two is perhaps on this very account best qualified to render evident the conclusion with which we are here concerned, viz. *that one and the same auditory organ together with its auditory centre must produce an entirely different effect upon the mind according as this is more*

highly or lowly organized. The 'soul' is, as it were, played upon like an instrument by the musical nerve-vibrations of the auditory centre. The more perfect this instrument is the greater is the effect produced. The perception of music by the highest animals, such as the dog, cat, or horse, must be very imperfect as regards the purely formal relation between chords and successions of simple notes, because their mind is lowly developed, because their intellect cannot find any interest in following the manifold intricacies of the progress of 'parts.' It is not keen and acute enough even to perceive the varying distinctions between one 'timbre' of sound and another, for it has no purely mental interests. Only in the most crude and general manner are the souls of animals open to the emotional effects of music. Music impresses them as agreeable or disagreeable, and attracts them entirely irrespective of what we call the 'character' of a performance. The above-mentioned dog which followed the music of the fair was probably agreeably affected by every performance of the street band, whether it was in a major or minor key, whether it was a polka or a funeral march. So far as the dog was concerned the finer shades of difference, by which we are affected so powerfully, had no existence at all; it was only impressed by the sound, the mere pure *matter* of music, a thing which is of no importance to us as compared with the *form* of it. That which we admire most in music, and which chiefly excites our interest, is the originality and richness of musical forms, as Hanslick has so admirably shown in his interesting essay on 'The Beautiful in Music[1].' We are able to enjoy a symphony in a pianoforte arrangement, or, with sufficient practice, by merely reading the notes; and we appreciate not merely its formal relationship, but also its emotional effect and significance. By reading it we can be sent into a happy or a melancholy frame of mind, and we can fancy that we see in the composition the representation of moods of mind as distinguished from particular 'feelings.' Everyone will admit that, at any rate as regards this latter effect of music, even the highest animal can never have any idea, even though its hearing and its auditory centre were practised for the whole of its life; and this must be

[1] See also 'Sensation and Intuition' by James Sully, and 'The Power of Sound' by Edmund Gurney.

so because behind its auditory and musical sense there lies no correspondingly developed mind.

The same thing holds, although not to an equal extent, between the varied degrees of development reached by the human mind. If primitive man did not possess a mind like that of his descendants, if his intellect and every dependent power became far keener and deeper as the struggle for life went on through the course of ages, it follows that the faculty of perceiving music must also have been augmented.

It is therefore impossible that a lost Beethoven ever existed among primitive man, nay, I should even doubt whether one could be found among existing Australians or negroes. For the production of a Beethoven there is needed not only a highly developed musical sense, but also a rich and great soul, one that is infinitely sensitive; and we know by experience that such a nature is only to be found among the very highest intellects. But I will go further; I do not believe that the child of primitive man, if he were alive to-day, could be raised by education to the same level of musical understanding as that reached by our own children. He would fail for want of inherent power of mind.

Of course these opinions can never be confirmed, because primitive man is not to be found. But we still have the Australian native, although, so far as I am aware, the necessary investigations have never yet been made. But even if they were never carried out, it would nevertheless be certain that primitive man must have possessed lower mental faculties and especially a humbler intellect than civilized man: this conclusion is commonly accepted, and it is sufficient for my argument.

Hence we may assume that susceptibility to music must have increased during the intellectual evolution of mankind, so long, in fact, as the essential nature of the human mind was capable of being raised. It is impossible to decide upon the precise period in the history of a certain nation or group of nations at which the climax was reached; for we are by no means sure that the human intellect is not even now undergoing slow and imperceptible development. But as a mere suggestion, without any pretence to exactness, I will state that the people of 'antiquity,' viz. the ancient civilized nations of

the Mediterranean, had already, at the very dawn of their history, attained the highest level of intellectual development. If any further growth has occurred since then in European nations, it has certainly been so imperceptibly small that it could cause no sensible difference in the susceptibility of the human soul to music. The times which produced such legislators as Moses and Solon, poets like Homer and Sophocles, philosophers and men of science like Aristotle, Plato, and Archimedes,—times which created the Egyptian temples and pyramids and the statues of Greek gods, most undoubtedly display the achievements of the human intellect at its best. And an age which produced the gentle and forgiving Christian philosophy shows us that, as regards character and feeling, the human mind had attained the highest development.

We may therefore safely assume that the nations of 'antiquity' possessed a capacity for music in all respects equal to our own, and that the times during which the human intellect was raised, at least to any considerable extent, lie far behind them.

The fact however that the music of antiquity was so poor, depends, as we have seen, upon the complete distinction between music and musical talent: the latter is due, and due only, to the nature of the individual body and mind, while the former is also due to a slow process of development by means of tradition. Music is an invention and rests upon tradition,—the power on which depend the entire growth of culture, the development of language, of the sciences and their practical applications, and of every kind of art.

Painting and sculpture also have not been developed, viz. increased and perfected, because of any growth in the physical means by which we practise them. The human eye and the corresponding part of the brain, the visual centre, have certainly not been improved since the age of the lowest culture, or even since the times of primitive man. But the artistic acquirements of generations have been built one upon another until there arose the great art-palace of the present day with all its varied chambers. In this case it is even easier to prove that the instrument by which art has been invented existed in all its present perfection long before the invention had been made, and that it did not originate for the sake of art, but to be used as

a weapon in the great struggle for life. It is evident that the keenest vision is of vast importance for the preservation of the human species. Hence the arts of painting and sculpture are, in the sense above mentioned, merely the incidental accessory performance of a faculty never intended for such a purpose.

It is quite true that the beginnings of art can be traced far back to the times of the cave-dwellers; but whenever it began an immense period was required for its development,—a period which must have been especially long in the case of music.

It is almost impossible to realize that men with such high æsthetic instincts as those possessed by the ancient Greeks could have enjoyed the unisonal effect of accompaniment in the octave; and we can hardly believe that they were unable to invent music in two parts. And yet a long time elapsed before the gallant troubadours of Provence hit upon the idea of letting the melody be accompanied by another deeper-pitched voice, originally moreover in succession of fourths and fifths, so very unpleasant to us at the present day, but which may even now be occasionally heard in the street music of Brittany.

It is not my intention to follow the slow and gradual evolution of music; for this has been clearly shown by the excellent work of other writers. But in concluding I wish to repeat that this evolution does not depend upon any increase of the musical faculty or any alteration in the inherent physical nature of man, but solely upon the power of transmitting the intellectual achievements of each generation to those which follow.

This, more than anything, is the cause of the superiority of man over animals—this, and not merely human faculty, although it may be admitted that the latter is much higher than in animals. And even if we were compelled to believe that human faculty has reached its limits and can never be increased again, even then we need not despair of the almost boundless progress of mankind. For each generation always starts from the acquirements of the preceding one; and the living child placed from the very first by tradition upon a somewhat greater height of intellectual achievement than that of his predecessors, is then able, with the same powers, to climb yet higher up the steep slope of the most advanced civilization. Hence, even if our intellectual powers have reached the highest possible stage, human civilization will nevertheless advance, however far we

may look forward,—the conquests of the mind of man will never cease.

Lastly I trust that the scientific man may be excused if, in this essay, he has entered into what may appear to be a very distant region. Nevertheless it was a purely scientific question which led him into this inquiry—the question of the hereditary transmission of acquired characters. He attempted to explain, without any transmission of the results of practice, the existence of those human faculties which cannot be explained by the process of selection. This led to the explanation of the origin of the musical sense which has been adopted in this essay. Perhaps the opinions of a biologist may not be altogether devoid of interest for the philosopher and the musical critic. The questions treated of lie on the boundary between science and philosophy, and can hardly be solved from either province alone.

XI.

Remarks on Certain Problems of the Day.

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XI.

REMARKS ON CERTAIN PROBLEMS OF THE DAY.

The following essay was originally intended as an answer to the criticisms which Professor Vines [1] brought forward against certain of my views, shortly after the publication, in an English form, of a collected edition of those essays of mine which appeared in Germany during the years 1881–1889 [2].

This answer has been published in German because similar objections have been urged by German writers, and I further hope that this essay may perhaps serve to render clearer some of the problems with which it deals. Much might have been added on the points here referred to, but the occasion, and the nature of the essay itself, called for a certain amount of restriction, and enforced a concentrated treatment of the most important subjects.

Professor Vines commenced his article by a criticism of that attribute of immortality which I have claimed both for unicellular organisms and for the reproductive cells of multicellular beings. If I rightly understand the English professor, he does not contest the truth of this view, but he fails to find in my book a satisfactory explanation of the process by which the immortal organisms gave rise, in the course of their phyletic development, to mortal descendants. The first difficulty which presents itself is to understand how the mortal heteroplastides can have been evolved from the immortal monoplastides or homoplastides. The explanation of this process, given in my book, is the only one which seems applicable to the

[1] 'Nature,' Oct. 24, 1889, p. 621 et seqq.
[2] See Vol. I of the present Edition.

to a stand-still? To my mind the descent of the immortal to the condition of mortality, is less to be marvelled at than the fact that monoplastids and germ-cells have remained immortal. The slightest change in the properties of living matter might involve such a descent, and certain essential peculiarities in the composition of this substance must be most rigidly maintained, in order that the metabolic cycle may sweep on with perfect smoothness, and raise no obstacle against its own persistence. Even if we know nothing further of these essential peculiarities of structure, we may at least maintain that the rigorous and unceasing operation of natural selection is necessary to maintain them. Any deviation from this standard ends in death. I believe that I have shown that organs which have ceased to be useful become rudimentary, and ultimately disappear owing to the principle of panmixia alone,—not because of the direct effect of disuse, but because natural selection no longer maintains them at their former level. What is true of organs is also true of their functions; for function is but the expression of certain peculiarities of structure, whether we can directly perceive the connection or not. If then the immortality of unicellular beings rests on the fact that the structural arrangement of their substance is so accurately adjusted that the metabolic cycle always comes back to the same point,—why should, or rather, how could this property of the protoplasm, which is the cause of immortality, be retained when it ceased to be necessary? And clearly it is no longer of use in the somatic cells of heteroplastids. From the moment that natural selection relaxed its hold upon this property of the protoplasm, the power of panmixia began to be felt, and ultimately led to its disappearance. Prof. Vines will probably ask how this process can be conceived. I answer, quite simply. Let us suppose that certain individuals appeared among the monoplastids with such variation of the chemical or molecular characters, that the continuous recurrence of their metabolic cycle came to an end, so that natural death became a necessity. These individuals could never give rise to a persistent variety. But if individuals with a similar variation in their somatic cells arose among the heteroplastids, no detriment would be felt by the species: the body-cells would indeed die, but the undying germ-cells would secure the continuance of the species. By

means of the distinction between somatic and germ-cells, natural selection was enabled to direct its attention, to speak metaphorically, to the immortality of the germ-cells, and to an entirely different range of properties among the somatic cells, such as the capacity for movement, irritability, increased powers of assimilation, &c. &c. We do not yet know whether an increase in these properties is directly connected with a change of constitution involving the loss of immortality, but it is not impossible that this may be the case; and, if so, the somatic cells would have ceased to be immortal more quickly than if panmixia were the only agency at work.

I have adduced in my fourth essay[1] the cases of the Volvocinean genera, *Volvox* and *Pandorina*, as examples of the differentiation of the lowest heteroplastids from the homoplastids. All the cells of *Pandorina* are similar and perform similar functions. *Volvox*, on the other hand, consists of somatic and germ-cells, and it is here that we should expect the introduction of natural death. Dr. Klein's recent observations[2] show that this, as a matter of fact, takes place: as soon as the germ-cells are matured, and have left the body of the Alga, the flagellate somatic cells begin to shrink, and in one or two days are all dead. This is all the more interesting because the somatic cells fulfil nutritive functions for the aggregate. It is true that they are not alone in performing the office of assimilation, for the germ-cells also contain chlorophyll; but the immense size which the latter attain in *Volvox* can only be explained on the supposition that they receive nutriment from the somatic cells. These cells are so constituted that they assimilate, but when once the spherical colony has attained its definite size they have ceased to grow. By means of a fine protoplasmic network the body-cells pass on to the germ-cells all the nutriment they acquire from the decomposition of carbon dioxide and water, and when the reproductive cells are mature they die. In this case adaptation for supplying nutriment to the germ-cells may have hastened the introduction of death among the somatic cells, inasmuch as some structure may

[1] See Vol. I, p. 163.

[2] Ludwig Klein, 'Morphologische und Biologische Studien über die Gattung Volvox.' Pringsheim's Jahrbücher für wissenschaftliche Botanik, Bd. XX. 1889.

have arisen in the latter which rendered possible more energetic assimilation, but which was accompanied by an expenditure of nutriment, and which, after the lapse of a certain time, involved the complete cessation of assimilation, and consequently the death of the organism.

The conception of a change in the protoplasm which involves the loss of immortality is to my mind no more improbable or more difficult than the commonly received view of the differentiation of somatic cells which gradually takes place in their phylogeny, by which they are enabled to assume various natures, i. e. absorptive, secretory, muscular, nervous, &c. An unchangeable immortal protoplasm does not exist, only an immortal 'form of activity' in organic matter.

Thus my former statement, that unicellular organisms and the reproductive cells of higher forms do not suffer natural death, is maintained in its entirety; and I know of no better way to give expression to this idea than to say that such structures possess immortality, that is real, true immortality, not the phantastic, visionary immortality of the old Greek gods. If then death from internal causes has no existence for the organisms and structures in question, we can nevertheless maintain with absolute certainty that every one of them will come to an end, not indeed by the operation of forces from within, but because the external conditions which are necessary for the constant renewal of vital activity must at some future time themselves cease to be. The physicist predicts that the circulation of water on the earth will at some time inevitably cease, not because of any change in the nature of water, but because external conditions will render impossible this kind of movement of its particles.

Professor Vines then attacks my views on embryogeny. He finds it 'not a little remarkable that Professor Weismann should not have offered any suggestion as to the conception which he has formed of the mode in which the conversion of germ-plasm into somatoplasm can take place, considering that this assumption is the key to his whole position[1].' He finds in this the same difficulty as in the phyletic development of multicellular from unicellular organisms. He concludes his objection with the words, 'There is really no other criticism to be made on an

[1] 'Nature,' Oct. 1889, p. 623.

unsupported assumption such as this, than to say that it involves a contradiction in terms[1].' By this Professor Vines means that the eternal cannot, from its very nature, pass into the mortal, as it must do, if the perishable soma is derived from undying germ-cells. It is obvious that this objection rests upon the same confusion between immortality and eternity which has been already rendered clear. I do not wish to reproach Professor Vines with regard to this confusion; some years ago I encountered the same objection, and did not at once see where the answer lay. We have hitherto been without a scientific conception of immortality: we must understand by this term—not life without beginning or end—but life which, when it has once originated, continues without limit, accompanied or unaccompanied by modification (viz. specific changes in unicellular organisms, or in the germ-plasm of multicellular forms). This immortality is a movement of organic material, which always recurs in a cycle, and is associated with no force that tends to arrest its progress, just as the motion of planets is associated with nothing which tends to arrest their movement, although it had a beginning and must at some future time, by the operation of external causes, come to an end.

Further on, Professor Vines says, 'I understand Professor Weismann to imply that his theory of heredity is not—like, for instance, Darwin's theory of pangenesis—"a provisional or purely formal solution[2]" of the question, but one which is applicable to every detail of embryogeny, as well as to the more general phenomena of heredity and variation[3].' I have indeed, in contradistinction to my own attempt to give a theoretical basis to heredity, spoken of Darwin's pangenesis as a purely formal solution of the question; and perhaps I may be allowed to give a short explanation of the expression, for I fear that, not only Professor Vines, but many other readers of my essays may have misunderstood me. On the one hand I am afraid that they may have found in my words a tacit objection to Darwin's pangenesis, an objection which I did not at all intend, and, on the other, that I was inclined to overstate the value of my own theory.

There are, I think, two kinds of theory which may be con-

[1] 'Nature,' Oct. 1889, p. 623.
[2] See Vol. I, p. 168.
[3] 'Nature,' Oct. 1889, p. 623.

veniently distinguished as *ideal* and *real*. Practically it is found that they are seldom sharply discriminated; often both kinds occur combined in one and the same theory: nevertheless they should be clearly distinguished. The *ideal* theory seeks to explain phenomena by any arbitrarily chosen principle, quite apart from the question whether the principle has any actual existence or not[1]. The ideal theory only seeks to show that there are hypotheses on which the phenomena in question are explicable. Real theories however are not content with plausible hypotheses, but endeavour to include only those which possess some degree of probability: they attempt to give not merely a formal solution, but, if possible, the correct one. Sir William Thomson has attempted to explain the dispersion of rays of light, by imagining the existence of molecules which are composed of concentric hollow spheres, arranged one inside the other and connected together by springs. But this distinguished physicist never for a moment believed in the existence of real molecules, provided with springs; he wished to show that existing conceptions were capable of rendering intelligible the phenomena of dispersion. Obviously Darwin's pangenesis was conceived in this spirit, and was therefore called by him 'provisional'; although in later life he may have come to attach real worth to the theory. I consider the gemmules to be a deliberate invention, like Sir William Thomson's molecules provided with springs, which have no claim to reality: the gemmules merely serve to show the sort of suppositions we must make in order to understand the phenomena of heredity.

Ideal theories are by no means useless. They are the first and often the indispensable steps which we must take on our way to the understanding of complex phenomena. They form the foundation upon which real theories can gradually be raised. Above all, they supply the impulse to re-examine again and again the phenomena they attempt to explain. I should probably never have been led to deny the inheritance of acquired characters, if Darwin's pangenesis had not shown me that the belief in such transmission involved an assumption so

[1] The two philosophers Herbart and Lotze have named these two types of theory '*fiction*' and '*hypothesis*': the former term agrees with *ideal* in expressing the consciousness of unreality.

difficult to realize as that of the giving off, circulation, and accumulation of gemmules.

I do not even now assert that Darwin's pangenesis may not possibly contain a nucleus of truth. De Vries, in his recent exceedingly interesting work[1], has shown that the ideal (impossible) pangenesis of Darwin may be modified into a real (possible) theory, by making a few, although very profound, modifications. He accepts my contention that acquired or somatogenetic changes cannot be inherited, and thus dismisses precisely that part of pangenesis, which, in my opinion, lies outside the limits of possibility, namely the throwing off, circulation and collection of the gemmules. The future will decide whether the assumption of modified gemmules furnishes a better explanation of the facts of heredity than my hypothesis.

But under any circumstances, I do not in any way presume to consider that the whole problem of heredity is solved. I have undertaken investigations on some of the more important points raised by the problem, and consequently have been led to formulate certain fundamental principles in order to explain some of the phenomena of heredity; but no one knows more thoroughly than I do how far we still are from definitely and completely understanding, not only every detail of embryology, but the more general phenomena also. My endeavour has been to substitute a 'real' theory for the 'ideal' theory which has existed hitherto; and I therefore took pains in thinking out conceptions which should, as far as possible, correspond with the results of actual observations. There is undoubtedly a material basis of heredity in the egg, which can with equal certainty be transmitted from nucleus to nucleus, and it may be modified, or may remain unchanged in the process. Furthermore, the supposition that this substance is able to impress a specific character on the cell involves nothing that appears to be impossible or non-existent. So far from this being the case, we are even now able to prove that the character is thus actually stamped upon the cell, although we cannot understand the way in which the process happens. Finally, my view that germ-plasm in an inactive condition potentially contains certain tendencies of the somatic cells which are ultimately derived from it, stands upon a firm basis, for we know that ancestral

[1] Hugo de Vries, 'Intrazellulāre Pangenesis,' Jena, 1889.

characters can be inherited in a latent state, and we also know that the process of inheritance is associated with a certain substance, the idioplasm of the germ-cell. Such idioplasm must therefore be in an inactive state during the period of latency.

If it can be demonstrated that such principles suffice to explain the phenomena of heredity, we have made an essential advance beyond the ideal theory of pangenesis, which is built up on suppositions which do not correspond with realities. Perhaps the path which I have struck out may by degrees lead to a satisfactory solution of the numerous questions connected with heredity; perhaps further investigation may show that we are on the wrong track and must abandon it; what the future of the question may be no one can foretell. My thoughts upon heredity are not final, but rather serve as a starting-point for further thought; they constitute no complete theory of heredity which claims to have satisfied all sides of this most complex subject; they are rather 'researches' which, if fortune favours, will, sooner or later, directly or indirectly, lead to the formation of a real theory. I have expressly stated this in the Preface to the English Edition of my collected essays.

In the same place I have emphasized the fact that my book did not originate as a whole, but is made up of a series of researches, each of which, I hope, marks some advance, each of which is built up on the foundation provided by the previous one. It contains to some extent the history of the development of my views as they have gradually shaped themselves in the course of nearly ten years' work. It is therefore unreasonable to extract ideas from the earlier essays and to make use of them against the later views. All the essays have been left unchanged, and 'certain errors of interpretation left uncorrected[1],' because otherwise the intimate connection which exists between the essays could not have been distinctly traced.

The objections which Professor Vines urges against my theory of the Continuity of the Germ-plasm entirely depend, in my opinion, on an unintentional confusion of my ideas; for he applies the views of the second essay to the ideas in some of the later ones, with which they do not harmonize. I will attempt to explain this in few words: in my second essay[2] (1883)

[1] See Author's Preface to First Edition, Vol. I, p. iv.
[2] See Vol. I, p. 67.

I contrasted the body (*soma*) with the germ-cells and explained heredity by the supposition of a material basis residing in the germ-cells ; i. e. the germ-plasm, which is continuously passed on from one generation to another. When the essay was being written, I was not aware that this germ-plasm existed only in the nucleus of the egg-cell, and I was therefore able to contrast the entire substance of which the egg-cell consists, or the germ-plasm, with the substance which composes the body-cells, hence called somatoplasm. In the fourth essay[1] (1885) I expressed my conviction, which agreed with that shortly before expressed by Strasburger and O. Hertwig, that the substance of the egg-nucleus, or, more precisely, the chromatin of the nuclear loops, formed the material basis of heredity, the body of the cell being only nutritive and capable of being moulded by forces emanating from the nucleus, but in no way formative. Together with the two above-mentioned writers, I transferred the conception of idioplasm—introduced at that time by Nägeli, although defined by him in an essentially different manner,—to the material basis of heredity in the egg-nucleus, and submitted that not only in the ovum but in every cell the chromatin of the nuclear thread was the idioplasm which dominated the whole cell, and impressed its own specific character upon the originally indifferent cell-body. From this time I no longer spoke of the cells of the body as simply somatic protoplasm (somatoplasm), but in each cell I distinguished, first, between the idioplasm, or substance which gives to the nucleus its power of predisposition, and the body of the cell or cytoplasm ; and, secondly, I distinguished between the idioplasm of the egg-nucleus and that of the nucleus of somatic cells. The idioplasm of the germ- or sperm-cell alone was called germ-plasm (idioplasm of reproductive cells), while the idioplasm of the somatic cells was called somatic idioplasm. Embryogeny, in my opinion, depends only on changes in the idioplasm of the egg-nucleus, i. e. changes in the germ-plasm. In my fourth essay there is a description of the manner in which the idioplasm of the egg-nucleus divides, in many species, at the first segmentation, each half undergoing certain regular modifications of nuclear substance, so that neither daughter-cell possesses the collective hereditary tendencies of the species, but one

[1] See Vol. I, p. 163.

contains those of the ectoderm, and the other those of the endoderm. The later stages of embryogeny depend on a continuance of such regular modifications of idioplasm. Each fresh division sorts out fresh predispositions, previously mixed in the nucleus of the mother-cell, until at length the full number of embryonic cells have come into existence, each with an idioplasm in its nucleus which stamps the specific histological character upon the cell.

I fail to understand why this idea presents such remarkable difficulties to Professor Vines. In most species the separation of the sexual cells takes place late in the embryogeny. Now in order to maintain the continuity of germ-plasm from one generation to another, I have supposed that, at the first division of the ovum, not all the germ-plasm (i.e. idioplasm of the first ontogenetic stage) becomes changed into idioplasm of the second stage, but that a minute portion of it persists unchanged included in one or other of the daughter-cells, where it remains inactive, intermingled with the nuclear idioplasm ; I have further assumed that in this condition it is transmitted through a longer or shorter series of cell-generations until at length it reaches certain cells on which it impresses the characters of germ-cells, and in these it resumes its activity. This view is not entirely devoid of support ; for it is in some degree confirmed by actual observations, especially by those on the remarkable wanderings through which the germ-cells of Hydroids pass, after starting from their original place of formation [1].

But let us leave the consideration of the degree of probability which my theory may possess, and consider only its logical accuracy. Professor Vines says, 'The fate of the germ-plasm of the fertilized ovum is, according to Professor Weismann, to be converted in part into the somatoplasm (!) of the embryo, and in part to be stored up in the germ-cells of the embryo. This being so, how are we to conceive that the germ-plasm of the ovum can impress upon the somatoplasm (!) of the developing embryo, the hereditary character of which it (the germ-plasm) is the bearer? This function cannot be discharged by that portion of the germ-plasm of the ovum which has be-

[1] Weismann, 'Die Entstehung der Sexualzellen bei den Hydromedusen,' Jena, 1883.

come converted into the somatoplasm (!) of the embryo, *for the simple reason that it has ceased to be germ-plasm*, and must therefore have lost the properties characteristic of that substance. Neither can it be discharged by that portion of the germ-plasm of the ovum which is aggregated in the germ-cells of the embryo, for under these circumstances it is withdrawn from all direct relation with the developing somatic cells. The question remains without an answer[1].'

I believe, however, that the answer is to be found above. I know nothing of the 'somatoplasm' of Professor Vines: my germ-plasm, or idioplasm of the 1st ontogenetic stage, is not modified into the 'somatoplasm' of Professor Vines, but into idioplasm of the 2nd ontogenetic stage, and then into that of the 3rd, 4th, 5th, and so on up to the 100th and 1000th stage; and each stage of idioplasm confers its own specific character upon the cell in the nucleus of which it lies.

Professor Vines also criticises my views as to the idioplastic nature of the nuclear substance (the chromatin granules in the nuclear loops, &c.). He maintains that it is as easy to speak of the continuity of the cell-body as the continuity of the nuclear substance, and that hereditary peculiarities can be as well transmitted to the offspring by the former as by the latter.

I can quite understand why a botanist should take this view, and indeed, in bringing it forward, Professor Vines does not stand alone. Waldeyer[2] maintained, in 1888, that established facts did not justify us in regarding the nuclear loops as possessing an idioplastic nature. Among other zoologists, Whitman[3] has pronounced very decidedly against the idioplastic nature of the nucleus, and in their recent work, Geddes and Thomson[4] have done the same.

The facts which suggested to my mind that the nuclear loops are the material basis of heredity,—in fact the idioplasm,—are enumerated in my fourth essay[5]. They were chiefly the observations of Van Beneden on the process of fertilization in the

[1] 'Nature,' Oct. 1889, p. 623.

[2] Waldeyer, 'Ueber Karyokinese und ihre Beziehung zu den Befruchtungsorganen,' Archiv für Mikr. Anatomie, Bd. XXXII. 1888.

[3] Whitman, 'The Seat of formative and regenerative Energy,' Boston, 1888.

[4] Geddes and Thomson, 'The Evolution of Sex,' London, 1889.

[5] See Vol. I, p. 163.

egg of *Ascaris megalocephala*, the observations of Strasburger on the fertilization of the egg-cell in phanerogams by means of the nucleus alone, and the experiments of Nussbaum and Gruber on the artificial division of Infusoria. To these may be added certain other considerations of essential importance, viz. the occurrence of karyokinesis, and the fact that the formation of polar bodies by the ova of animals can be rendered intelligible only on the assumption that the idioplasm resides in the nucleus. The formation of polar bodies involves the division of the nuclear substance of the egg into two halves similar in quantity, but the cell-body itself is divided into two entirely dissimilar portions, the relative sizes of which differ in different species. The essential part of this expulsion of polar bodies from the ovum, must lie in the division of the nuclear substance, and not in the division of the cell. These facts and considerations, in conjunction with others, completely convinced me that the nuclear substance is the sole carrier of hereditary tendencies: the view which I expressed ten years earlier (1873), of the physiological equality (Homodynamy) of the nuclei of both male and female germ-cells, became to my mind a certainty, and I then advanced the theory of fertilization which is to be found in my fourth essay. No one, as far as I know, with the single exception of Strasburger, has expressed similar views on the essential nature of fertilization, at any rate with regard to the homodynamy of the sexual nuclei. The distinguished observer E. van Beneden, to whom we owe so much of our knowledge of the processes of fertilization, has maintained his belief in the old view which looks upon fertilization as the union of two elements which are essentially opposed to each other. He is unable to free himself from the dominant idea, so firmly embedded in the biological mind, that sexual difference is something fundamental, and an essential principle of life itself. To him, the fertilized ovum is a 'hermaphrodite' being, which unites in itself both male and female entities,—an idea which has commended itself to many authorities, but an idea of which the logical outcome forces us to regard all the cells of the body as hermaphrodite. Van Beneden was at the same time swayed by the opinion, which is shared by so many workers in other lands, that fertilization is a process of rejuvenescence, without which terrestrial life could not continue. Many observers still

cling to this view, and Maupas[1] has recently claimed to have found a proof of its soundness by showing that it is essential for Infusoria to conjugate (sexual reproduction) from time to time.

This contention forms a striking example of the difficulty with which even scientifically trained minds can shake off deeply rooted convictions. Although it must be clear to every one that unicellular organisms are immortal, although Maupas has himself produced superabundant proofs that the reproduction of Infusoria by fission can go on without ceasing, and although he maintains that 'les cycles évolutifs des Ciliés peuvent se succéder à l'infini' (p. 437), nevertheless the power of the old tradition of the necessity of death is so strong in him that he is incapable of recognizing this simple fact. Rather than adopt the views propounded by others, he prefers to accept the hypothesis that unicellular organisms are really mortal and are subject to natural death, but that this is kept in abeyance and postponed by the influence of conjugation.

If we ask, whence comes this idea of the necessity of death, we receive the answer,—from our experience of man and the higher animals and plants. If we further ask, why has it hitherto been entirely overlooked that among these organisms certain parts of the body (the reproductive cells) are endowed with immortality, the answer is,—because we have only recently come to know and completely appreciate the facts of reproduction, and therefore have only just arrived at a correct estimate of them, and are now for the first time able to recognize in our reproductive cells, the undying parts of our individuality.

For how long then will reproduction be regarded as a dynamical process, as a stimulus, as 'the spark in the powder cask,' or in biological language the vitalizing of the egg? This conception is directly derived from the old vital force of earlier times, and it is the unrecognized reflection of this latter idea which influences many writers, and which, proteus-like, continually appearing in new forms, evokes the belief in a necessity for the rekindling of life.

If we lay aside preconceived notions and simply review the

[1] E. Maupas, 'Le rajeunissement karyogamique chez les Ciliés,' Arch. Zool. expér. et générale, 2 sér., Tom. vii. Nr. 1, 2, et 3, 1889.

facts of the case, we see, on the one side, unicellular animals which continually increase by division, and, on the other, multicellular animals which are differentiated into somatic and germ-cells,—animals in which the body dies, while the reproductive cells possess the same power of unlimited increase by division that is possessed by unicellular beings. But what leads us to consider that the capacity for continuous reproduction is rendered possible by the fusion of the essential material of one organism with that of another, such as we see in both conjugation and fertilization? Nothing but the unconscious tradition of the inevitability of death. Maupas thinks that he has proved the existence of natural death among the Infusoria, since he has shown by his investigations,—excellent as far as observation is concerned,—that, from time to time, conjugation must make its appearance, or the colony would die out; but he forgets that as a matter of fact under natural conditions, the possibility of conjugation is granted, and that thus the so-called natural death does not appear more often in nature than in the case of those metazoan ova which fail to meet with a spermatozoon. The Infusorian which has not conjugated gradually disappears, like the animal egg which remains unfertilized; and the so-called 'senile degeneration' (Maupas) of the former exactly corresponds to the gradual decomposition and dissolution of the latter, a process which was described long ago, in a species of *Moina*, in one of my memoirs on the Daphnids. Conjugation, no less than fertilization, is undoubtedly a process of vast importance; but I believe that its significance lies in the maintenance and continual intermingling of individual variations, or it may be that some other advantage is conferred which acts for the preservation of the species. In any case nature attaches great importance to it, and seeks to ensure it, for each species, to the greatest possible extent. For this purpose she has made provision that the periodical recurrence of the process should affect as many individuals as possible. If however, in spite of every provision, unfavourable circumstances should bring it about that certain individuals have no part in the process of conjugation, is it to be wondered at that nature should care nothing for their preservation? Or, to speak less figuratively, we must not be surprised to see that means are taken to prevent the unlimited increase of those

individuals which are less favourably placed for the continuation of the species. How, in fact, can this be otherwise, since, in Infusoria, the unlimited continuance of life is bound up with conjugation, just as in the ova or spermatozoa of higher organisms, it is dependant on fertilization. It might be objected that the cases are different, inasmuch as the germ-cells which fail to be fertilized perish for lack of nourishment, while the Infusoria which fail to conjugate experience no such difficulty: when therefore they come to an end after a certain number of generations, their death must be due to the working of other causes. But in the above-mentioned Daphnid *Moina rectirostris* when copulation has not taken place the unfertilized egg is not laid at all. It retains the very position in the ovary which it would occupy during development, and it is placed under the most favourable conditions of nutrition. For some time it retains its vitality, but if still unfertilized, it ultimately dies and undergoes dissolution, being finally completely reabsorbed by the surrounding epithelial cells of the ovary. The egg is so constituted that it remains alive for a certain time awaiting fertilization, and then, in spite of the most favourable conditions of nutrition, it perishes. If copulation be delayed in the nearly allied *Moina paradoxa*, the unfertilized eggs are laid and die at once, so that their material is lost to the animal. It is obvious that the arrangement in *Moina rectirostris* is a special adaptation enabling the organism to utilize the material of the large eggs which, unless fertilized, are incapable of further development. We do not know what kind of an arrangement it is which involves the death of the egg although surrounded by such favourable conditions of nutrition, any more than we know what causes the fate of the unconjugated Infusorian: the facts however show that some arrangement must exist to produce such results. The continued life of an egg requiring fertilization, is dependant on fertilization; that of an Infusorian needing conjugation, on conjugation.

The experiments of Maupas seem to show that Infusoria are adapted for fertilization, that periodical conjugation is one of the conditions of their life, like food and oxygen. But it is a fallacy, only explicable on the ground of deep-rooted prejudice, to argue from this that they are really mortal, and that their actual immortality depends on the magic of conjugation. One

might just as well maintain that food is the cause of Infusorian immortality, inasmuch as death ensues when food is withheld. I believe that the essential, fundamental, and original peculiarity of living matter was the power to assimilate and to grow without limit. On this depends the existence of the whole organic world: it is a primary power, not a secondary one, and cannot have been conjured up afterwards in the organism by any refined artifice, call it conjugation, fertilization, or anything else. It must have been present from the very beginning of life on the earth. How otherwise could life have persisted up to the first appearance of conjugation or fertilization? For there can be scarcely any doubt that neither of these processes is found in the lowest organisms at present known to us. I therefore think that the loss of this fundamental power of unlimited growth must be regarded as a secondary adaptation, called forth by certain special circumstances which rendered it necessary for achieving the combination of different individual hereditary tendencies. When, therefore, certain writers speak of these processes of conjugation and fertilization as a rejuvenescence, in the sense of a renewal of vital energy, I can only believe that they are upholding a long-vanquished and mystical principle. It is quite otherwise if we speak of the conjugation of Infusoria as a rejuvenescence in the sense of a dissolution and re-formation of many parts: this is a process which may depend throughout on well-known natural forces, and which makes its appearance not only in conjugation but in division also. I have no objection to raise against this kind of rejuvenescence; in fact the continual repetition of such regeneration among these undying organisms, exposed, as they are, to constant wear and tear, becomes a necessary assumption.

In my fourth essay, the idea of fertilization being regarded as a process of rejuvenescence, in the sense of a renewal of vital force, is opposed, and the converse view is clearly enunciated. To condense my argument into a sentence,—we ought not to speak, as formerly, of the two conjugating nuclei of the germ-cells as male and female, but as *paternal* and *maternal*; they are not opposed to each other, but are essentially alike, differing only as one individual differs from another of the same species. Fertilization is no process of rejuvenescence, it is nothing more than a mingling of the hereditary tendencies of two individuals.

These tendencies are exclusively contained in the nuclear loops; the cell-bodies of the spermatozoon and ovum are in this respect indifferent, and serve only as the nutritive material which is formed and transformed in a definite way by the dominating idioplasm of the nucleus, as clay is moulded by the hand of a sculptor. That the egg and the spermatozoon differ so greatly in appearance and function, and that they mutually attract each other, depend on secondary adaptations, which ensure that they shall find each other, that their idioplasm or nuclear substance shall come into contact, while, at the same time, a certain amount of nutriment shall be provided for the embryogeny, &c. &c. And just as the differentiation of cells into male and female reproductive elements is secondary, so is that of male and female individuals: all the numerous differences in form and function which characterize sex among the higher animals, all the so-called 'secondary sexual characters,' affecting even the highest mental qualities of mankind, are nothing but adaptations to bring about the union of the hereditary tendencies of two individuals.

These are briefly the ideas on fertilization which I indicated in the year 1873, and which I published in a detailed and definite form in 1885, after the discoveries of Van Beneden on the morphological processes which take place during the fertilization of the egg of *Ascaris*[1]. Towards the end of the essay I used these words, 'If it were possible to introduce the female pronucleus of an egg into another egg of the same species, immediately after the transformation of the nucleus of the latter into the female pronucleus, it is very probable that the two nuclei would conjugate just as if a fertilizing sperm-nucleus had penetrated. If this were so, the direct proof that egg-nucleus and sperm-nucleus are identical would be furnished. Unfortunately the practical difficulties are so great that it is hardly possible that the experiment can ever be made; but such want of experimental proof is partially compensated for by the fact, ascertained by Berthold, that in certain Algæ (*Ectocarpus* and *Scytosiphon*) there is not only a female, but also a male parthenogenesis; for he shows that in these species the male germ-cells may sometimes develop into plants, which however are very weakly[2].'

[1] See Vol. I, Essay iv, p. 163. [2] See Vol. I, pp. 252, 253.

Since then I have made the attempt to fertilize the ovum of a frog with the nucleus of another; the experiment did not succeed, and we could scarcely expect it to do so, considering the very considerable amount of injury caused by transferring a nucleus into another egg.

Boveri[1] has been more fortunate; for he succeeded in finding an object which permitted the converse of my experiment. Adopting the method of R. Hertwig, he separated, by shaking, the nucleus from the ovum of an *Echinus*, and succeeded in rearing such denucleated eggs by the introduction of spermatozoa. A regular segmentation nucleus was formed from the spermatozoon which penetrated the egg, embryogeny followed its usual course, and the egg gave rise to a perfect but rather small larva, which swam freely about in the water, and lived until the seventh day.

This experiment is by itself sufficient to prove that the views on fertilization adopted by Strasburger and myself are correct, viz. that the nucleus of the spermatozoon can play the part of the nucleus of the egg, and *vice versa*, and that the older view to which Professor Vines[2] adheres, must be given up.

An interesting and important modification of Boveri's experiment, affords further support to the results obtained by him, and confirms—if indeed confirmation be necessary—the view which looks upon the nuclear substance as idioplasm, as maintained by O. Hertwig, Strasburger, and myself[3].

If the eggs of *Echinus microtuberculatus*, artificially deprived of their nuclei, be fertilized, not with the spermatozoa of their own species, but with those of another, *Sphaerechinus granularis*, *larvae are developed with the true characters of the last species only*, that is to say, nothing is inherited from the mother but everything from the father. The nuclear substance is the sole bearer of hereditary tendencies and by it the cell is governed.

I have explained the first polar body of the metazoan egg as the carrier of ovogenetic idioplasm which must be removed

[1] Boveri, 'Ein geschlechtlich erzeugter Organismus ohne mütterliche Eigenschaften.' Gesellsch. f. Morph. u. Physiol. München, 16 Juli, 1883.

[2] S. H. Vines, 'Lectures on the Physiology of Plants.' Cambridge, 1886, pp. 638-681.

[3] Cf. Kölliker, 'Die Bedeutung der Zellenkerne für die Vorgänge der Vererbung.' Z. f. W. Z. Bd. 42, 1885.

in order that the germ-plasm may become dominant. It is possible that this explanation may be incorrect. The latest observations on the conjugation of Infusoria, as recorded in the excellent works of Maupas and R. Hertwig, are opposed to my explanation, although the idea upon which it was formed is justified. Since it is the nuclear substance which gives to the cell its specific character, the egg-cell must before fertilization be dominated by an idioplasm distinct from that of the sperm-cell, for they are, up to this point, of different form and function. As soon however as fertilization is accomplished they both contain the same idioplasm, namely germ-plasm. Hence the earlier dominant idioplasm must be different from the later.

This fundamental idea upon which my interpretation of the first polar body was founded appears to be sound. One might perhaps imagine that the idioplasm of the egg was originally different from that of the spermatozoon, but that both possessed the power of changing into germ-plasm. But this would leave wholly unexplained the fact that parthenogenetic eggs extrude one polar body. Both facts become clear, if ova and spermatozoa are dominated until they reach maturity by different histogenetic idioplasmata, with which a small amount of germ-plasm is mingled, and if when the former are removed, the germ-plasm governs both cells. This process is in no way extraordinary and unparalleled ; for entirely analogous divisions of the idioplasm into halves of unequal quality, must take place hundreds of times in every embryogeny. However, I willingly admit that on this question the last word has not yet been spoken, and would merely add that my theory of heredity is not concerned thereby. As regards my theory, the significance of the second polar body, and not that of the first, is decisive. Even if it be demonstrated that my interpretation of the first polar body is erroneous, this would not interfere with the conception of the second as halving the number of ancestral germ-plasmata. I should then look upon the first division as merely leading up to the second, as a first step necessary for the reduction of the ancestral plasmata, although the reason for its necessity is not at present quite clear to us.

The occurrence of regular changes in the idioplasm during ontogeny, which I have urged, and which has been attacked

by so many writers, particularly by Kölliker[1], now appears to be justified. If the nucleus of a spermatozoon is capable of conveying to the body of an ovum which has lost its nucleus, the hereditary tendencies contained in itself, and of producing an organism with paternal characters only,—then we can scarcely conceive of ontogeny except as a series of regular changes of the idioplasm, advancing from cell-division to cell-division, and giving its special character to the body of every cell at every stage of growth, not only in respect to form, but also to function, and especially with regard to the rhythm of cell-division.

Professor Vines raises a further objection against my views on the origin of variation. In the fifth essay[2] I looked for the significance of sexual reproduction in the fact that it alone could have called forth that multiplicity of form which is met with among the higher plants and animals, and that constantly varying combination of individual variations, which natural selection required for the creation of new species. I still hold to the view that the origin of sexual reproduction in reality depends on the assistance which it affords to the working of natural selection, and I am entirely convinced that the higher development of the organic world was only rendered possible by the introduction of sexual reproduction. On the other hand, I am inclined to believe that Professor Vines is right in his contention that sexual reproduction is not the only factor which maintains the variability of the Metazoa and Metaphyta. I might have pointed out in the English translation of my essays that my views on this point had somewhat altered since the appearance of the German originals. My lamented friend, Professor De Bary, too early lost to science, had already directed my attention to those fungi which propagate themselves parthenogenetically, and which Professor Vines justly cites against this part of my view; but I wished on the grounds mentioned above to make no alteration in the essays. At the time when I wrote the essay in question (1886), I was well aware that my views on the causes of individual variation were

[1] Kölliker, 'Das Karyoplasma und die Vererbung: eine Kritik der Weismann'schen Theorie von der Kontinuität des Keimplasmas.' Z. f. W. Z. Bd 44, p 228, 1886.

[2] See Vol. I, p. 257.

possibly incomplete, and in order to expose the correctness of my view to the widest available test, I carried out its logical consequences as thoroughly as possible, and laid down the principle that species which propagate parthenogenetically have no power to develop into new species. Furthermore, about the same time, I began a series of experiments to test the truth of this statement as to the capacity for variation possessed by parthenogenetic species; these have been continued up to the present time, and on some future occasion I hope to make them public.

But even if, as seems at present very probable, sexual reproduction is not the only origin of individual variability in the Metazoa, no one will deny that it is the chief means of increasing these variations and of continuing them in favourable proportions. In my opinion, the importance of the rôle which sexual reproduction plays in shaping the material for the process of selection is scarcely diminished, even if we concede that some amount of individual variability can be called forth by direct influences on the germ-plasm. Even Professor Vines considers it probable 'that the absence of sexuality in these plants (the parthenogenetic higher Fungi) may be just the reason why no higher forms have been evolved from them; for in this respect they present a striking contrast to the higher Algae in which sexuality is well marked[1].'

But when Professor Vines says 'there can be no doubt that sexual reproduction does very materially promote variation[2],' he does not intend to imply that this statement is self-evident; for it is well known to him that prominent investigators, like Strasburger[3], see in sexual reproduction the reverse action, 'that of preserving the constancy of specific characters.' I accept with pleasure his agreement with my view, confirming the chief result of my fifth essay, which may be expressed as follows:—Sexual reproduction has arisen by and for natural selection, as the only means by which the individual variations can be united and combined in every possible proportion.

Again, with respect to the problem of the inheritance of ac-

[1] 'Nature,' Oct. 1889, p. 626. [2] 'Nature,' Oct. 1889, p. 626.
[3] Strasburger, 'Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung.' Jena 1884, p. 140.

quired (somatogenic) characters, Professor Vines finds himself opposed to me; for he regards such inheritance as possible. I have denied this because it did not appear to me self-evident, as had been previously assumed by every one, but rather utterly unproven; and because I believe that completely unproved assumptions of such importance should not be made, when they need such a number of improbable hypotheses to make them intelligible. I have tested, as accurately as possible, all the available evidence for such inheritance and have found that they possess no value as proofs. There is no inheritance of mutilations, and, up to the present time, these form the only real basis for the assumption of the hereditary transmission of somatogenic variations. If, in my last essay [1], I did not directly deny all possibility of such inheritance, Professor Vines should interpret that in my favour and not to my discredit: it is not the business of an investigator to maintain that a proposition, which he sets forth in accordance with the present state of our knowledge, must be accepted as an infallible dogma. Professor Vines finds the 'statements of opinion so fluctuating that it is difficult to determine what his position exactly is,' but he could have easily arrived at my views, if he had judged them by the last essay, instead of promiscuously contrasting isolated passages from eight essays, which occupied eight years in their production. The last essay is especially concerned with 'the supposed transmission of mutilations,' and, at the end of it, my verdict on the state of the problem of the inheritance of acquired (somatogenic) characters, is set forth as follows, 'The true decision as to the Lamarckian principle [lies in] the explanation of the observed phenomena of transformation. If, as I believe, these phenomena can be explained without the Lamarckian principle, we have no right to assume a form of transmission of which we cannot prove the existence. Only if it could be shown that we cannot now or ever dispense with the principle should we be justified in accepting it [2].'

The distinguished botanist, De Vries, has shown that certain constituents of the cell-body, for example the chromatophores of Algæ, pass directly from the germ-cell of the mother into the daughter organism, whilst, as a rule, the male germ-cell contains no chromatophores. This appears to be a possible case of the

[1] See Vol. I, p. 431. [2] See Vol. I, p. 461.

inheritance of somatogenic variations. In these low plants the difference between somatic and reproductive cells is slight, and the body of the egg-cell does not require to undergo a complete change in its chemical and structural characters in order to develope into the body of the somatic cells of the daughter individual. But what has this to do with the question whether, for instance, the skill of a pianist's fingers, acquired through practice, can be transmitted to his descendants? How does the result of this practice reach the germ-cells? Here lies the real problem which those who maintain the inheritance of somatogenic characters must solve.

The above-mentioned observations of Boveri on the ova of Echinoderms deprived of their nuclei, prove that the body of the egg-cell contributes nothing to inheritance. If then the inheritance of somatogenic characters takes place, it can only be by means of the nuclear substance of the germ-cells, that is through the germ-plasm, and that not in its patent, but in its latent state.

To abandon the Lamarckian principle certainly does not facilitate the explanation of phenomena, but what we need is not a merely formal explanation of the origin of species, although it may be the most convenient, but an attempt to discover the real and genuine explanation. We must endeavour to explain the phenomena without this principle, and I believe I have made a beginning in this direction. I have lately investigated the phenomena in a case where one would not expect to be able to dispense with the principle of modification through use, viz. in the case of artistic endowment[1]. I propounded to myself the question whether the musical faculty in man could be conceived of as arising without the increase of the original faculty by use. And I arrived at the conclusion that not only was this principle unnecessary, but that use has actually taken no share in the evolution of the musical sense.

[1] 'Gedanken über Musik bei Thieren und beim Menschen.' Deutsche Rundschau, October, 1889. Translated as the tenth essay,—the second in the present volume.

XII.

Amphimixis or the Essential Meaning of Conjugation and Sexual Reproduction.

With twelve Figures.

1891.

AMPHIMIXIS OR THE ESSENTIAL MEANING OF CONJUGATION AND SEXUAL REPRODUCTION.

PREFACE.

The present treatise brings to a conclusion a series of essays upon biological problems which have appeared in the course of the last ten years. They commenced with an enquiry into the duration of life, which led on to the question of the biological origin of death, and then turned to certain phenomena of inheritance and reproduction. They endeavoured to ascertain with certainty and to elucidate the real conditions of these phenomena, and to search out their essence and significance.

I shall attempt to explain, as clearly as possible, the close connexion existing between certain apparently isolated problems and the subject of this essay, which, although mainly concerned with so-called 'sexual reproduction,' is in reality the keystone of the whole structure. My object is to express more fully than before, the thought that the process which we are accustomed to regard as reproduction, is not reproduction only, but contains something *sui generis*, something which *may* be connected with reproduction proper, and in the higher plants and animals *is* so connected, but which is entirely separate in the lower organisms. I shall show that its significance does not lie in the maintenance of life but in the mingling of individualities.

To attain this object it will be necessary first to consider the remarkable morphological processes which accompany the maturation of reproductive cells, and, as far as possible, to seek for a true interpretation in the results of the most recent researches. Furthermore, it will be necessary to apply the ideas thus gained to the problem of conjugation, and to bring within the scope of the enquiry many other phenomena, such as the various kinds of reproduction, certain phases of the question of heredity, and the immortality of unicellular organisms, because these are most intimately connected and indeed mutually dependent.

Thus the thoughts which run through the previous essays resemble tangled threads which are gradually unravelled and are ultimately all woven together. I will only add the wish that the new conceptions to which these researches have led may prove a fruitful field for further investigations.

AUGUST WEISMANN.

LINDAU, LAKE OF CONSTANCE,
September 12, 1891.

AMPHIMIXIS, Etc.

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XII.

AMPHIMIXIS OR THE ESSENTIAL MEANING OF CONJUGATION AND SEXUAL REPRODUCTION.

Introduction.

For more than a decade biological enquiry has been engaged, with renewed energy, upon the problem of fertilization. When the brothers Hertwig, and Fol had taught and demonstrated the fusion of the nuclei of ovum and spermatozoon, and had further shown that, before fertilization, the egg undergoes certain preparatory changes resulting in the extrusion of the previously well-known polar bodies,—an attempt was made to understand the significance of these processes. What can this substance be that it requires to be thrown out from the ovum before fertilization? The first answer to this question depended on the then commonly received, although never clearly formulated opinion, that fertilization consisted in the union of two opposed forces,—of what may be described as a male and a female principle which, by their fusion, kindled anew that life which, without such rejuvenescence, must gradually come to an end. Considering the dominant theory as to the significance of fertilization, it was certainly justifiable to endeavour to look upon these bodies, expelled from the egg, as the bearers of one of the two antithetical forces, which were previously united in a single ovum, but which required to be separated in order to render the egg capable of fertilization. The polar bodies were thus looked upon as bearers of the male principle, by the removal of which the ovum became for the first time sexually differentiated, i.e. became female. This idea was not merely ingenious, it was the legitimate result of those indefinite ideas as to the essential nature of fertilization, which up to the present day have held

the field. Such a view must inevitably have been brought forward, if we were ever to arrive at a solution of the phenomena. I should certainly be the last to reproach the three savants who developed this hypothesis, although I have perhaps contributed something towards the proof of its unsoundness. The path to truth often lies through inevitable error.

I was, from the first, predisposed against the view of Minot, Balfour, and Edouard van Beneden, being influenced not only by certain isolated phenomena of inheritance, phenomena which were at a later time and with perfect justice, urged against it, but by the facts of inheritance taken as a whole, and by that conception as to the nature of fertilization to which I had even then been driven by these very facts, although unable to prove to myself, or to others, the soundness of my views.

We recognize two phenomena in amphigonic reproduction :— first, fertilization in its strictest sense, i. e. the fact that the ovum can only develope into a new being when it has united with the spermatozoon, after which union a 'vitalization of the egg' takes place (Hensen); secondly, the mingling of two hereditary tendencies. From the very oldest times it must have been observed that the peculiarities of the father as well as of the mother, may appear, and to an equal extent, in the children. Such transmission was conceived by some writers in a material sense; for they imagined a part of the substance of the mother or of the father as the basis of the body of the offspring; but it was also looked upon by others as simply the transmission of an impulse. Thus according to Aristotle the father confers the impulse to movement, while the mother contributes the material. Löwenhoek and the other 'spermatists' held that the semen alone forms the substance of the embryo, while his opponents, Swammerdam and Malpighi, the so-called 'ovists,' returned to Aristotle's view in so far that they believed that the mother gives rise to the substance, that is the ovum, while the male influence is limited to an 'aura seminalis,' which at the same time acts as the transmitter of movement.

Some writers regard inheritance by means of fertilization as a purely immaterial occurrence: thus Harvey, in his remarkable and minutely thought-out theory of heredity, imagined conception as a mental process, the folds of the mucous membrane lining the uterus corresponding to the

convolutions of the brain, and giving rise to the foetus under the influence of the semen; just as the brain, under the influence of external impressions, gives rise to thoughts. The term 'conception,' when figuratively applied to mental processes,—a term which has been obviously derived from conception on the part of a woman,—is here reversed, and used to explain the very process from which it is itself derived.

The same fundamental idea runs through all theories of fertilization up to the present time—the idea that the fertilization, i.e. the 'vitalization of the egg' is the important part, or, as we may say, the true purpose of sexual reproduction. The other side of this mode of reproduction has been comparatively neglected; the fact that two different predispositions, on the one hand that of the father, and on the other that of the mother, are by fertilization united in a single organism, has appeared as a secondary, but it is clear to some extent as an inevitable result of fertilization. Although this view is nowhere directly expressed, it is implied in all the utterances of both older and more recent writers. It must be admitted that so long as biologists were acquainted with no method of reproduction except the sexual, it was impossible to regard fertilization in any other light; it seemed that the co-operation of two individuals was indispensable in order to call a third to life, and it can scarcely have been surprising for this new organism to resemble its progenitors more closely than any other living being. But, even in recent times, when other methods of reproduction among plants and animals gained recognition, they did not at first cause any alteration in that view which regards fertilization as a process of vitalization, a calling forth of new life. In the case of all those higher beings which do not possess the power of asexual reproduction, it became evident that a certain complexity of organization excluded this method of increase. But then the asexual reproduction of the lower organisms is by no means always sufficient to fulfil every condition necessary for the maintenance of the species, and hence the origin of new individuals from unicellular germs capable of fertilization must have appeared as an essential advantage.

The first fact which tended to throw doubt on the view that fertilization is a renewal of life was the discovery of parthe-

nogenesis by C. Th. von Siebold[1] and Rudolph Leuckart[2]. When it was understood that, under certain circumstances, an egg could develope into a new individual without fertilization, this fact by itself was sufficient to show that a 'vitalization of the germ' could not be the object of fertilization, and could not be the cause of its appearance among living beings.

But it was long before the facts of parthenogenesis were generally accepted : indeed, in some circles they are not received at the present day. Only ten years ago, a prominent physiologist, Pflüger, held them to be unproved, and most botanists were inclined to doubt their existence among plants as well as animals ; for at that time parthenogenesis appeared to be wanting in plants and to have been erroneously believed in at an earlier date. Even when de Bary and Farlow had proved its undoubted existence in certain ferns, and others had found it in certain fungi, the Basidiomycetes, and the existence of parthenogenesis among some plants and many animals could no longer be denied, the attempt was made to crush the phenomena in the Procrustean bed of the received conception of fertilization. The ingenious French savant Balbiani had previously propounded the view that a certain occult and hitherto undiscovered fertilization took place at the seat of origin of the germs, in the ovaries and testes ; this fertilization was supposed to be in addition to the regular, recognized process, and, in cases of parthenogenesis, to compensate for it. So deeply rooted was the idea that new life could only arise by means of fertilization.

Even those investigators who no longer doubted the reality of parthenogenesis could not immediately and completely rid themselves of the received view, but endeavoured to make the new facts harmonize with the old ideas. Probably the most interesting attempt of this kind proceeded from Hensen, who indeed recognized that the 'views on sexual reproduction held up to that time had been overthrown' by means of parthenogenesis, inasmuch as the fundamental proposition as to sexual propagation had failed, viz., that one of the two sexual cells is by itself incapable of development. He nevertheless believed

[1] C. Th. von Siebold, 'Wahre Parthenogenesis'; Leipzig, 1856.

[2] Rudolph Leuckart, 'Zur Kenntniss des Generationswechsels und der Parthenogenesis bei den Insekten'; Frankfurt, 1858.

that we must 'not, on account of these isolated cases, underestimate the fact that the necessity for fertilization is predominant, and controls, to their most secret depths, the sources of life in animals and plants.' (Phys. d. Zeug. p. 160.) Hensen takes as his starting-point the fact that, among many animals, e. g. bees and wasps, parthenogenetic ova give rise to male individuals only, while in others, namely *Psyche* and *Solenobia* among Lepidoptera, and *Apus*, *Artemia*, and *Limnadia* among Crustacea, only females are thus produced; further, that in many Lepidoptera, as *Liparis*, single eggs possess a power of developing without fertilization, but only into male insects, or into caterpillars which afterwards die, or in other cases only as far as some earlier or later phase of embryonic life. From this he concludes that we are here 'dealing with a graduated series of phenomena,' 'with a gradation in the powers of development and of reproduction, that is of qualities which can be conveniently included in the term '*sexual force*.' Hence at that time V. Hensen considered, if I have rightly understood him, that the 'sexual force,' it is true, ordinarily reaches the egg by fertilization, but that it may, under certain conditions and in varying degrees, be included in the female germ-cells alone. Such ova can then undergo embryonic development without fertilization, and, according to the amount of contained 'sexual force,' can pass through a longer or shorter period of development; many reaching only a certain stage of segmentation, others the entire larval stage, while finally some may attain the condition of imago, with mature sexual organs. There are moreover various degrees of 'sexual force'; for Hensen considers that male offspring are produced by a smaller force than females. Eggs from which, without fertilization, males only can arise (bees), possess, in his opinion, a smaller 'sexual force' than those which without fertilization produce females. This view ultimately depends on the conception of the life-preserving effect of fertilization, since males alone cannot perpetuate the species; and hence eggs which, without fertilization, give rise to males, are unable to maintain the continuity of life, and would finally result in the disappearance of the species, just as eggs of still smaller 'sexual force' lead to the disappearance of the individual in the larval or even earlier embryonic stages.

A question arising out of this view, and one which Hensen doubtfully propounds, is 'whether the "sexual force" could increase to such an extent that males should become superfluous,' and whether parthenogenesis, like sexual reproduction, could continue, not only for a limited number of generations, but for an unending series.

As regards an answer to these questions Hensen was quite unbiassed and awaited the decision of facts; moreover, from his point of view, no theoretical impossibility attended any such increase in the female 'sexual force.' He was, at that time, far nearer to the most recent views on fertilization than those numerous investigators who held parthenogenesis to be the consequence of fertilization which had taken place in earlier generations, and who considered that its effect could never last through an unlimited series of generations, but that the vitalizing or rejuvenating effect of fertilization must be renewed from time to time, or the power of reproduction would be lost. On these fundamental views as to the 'vitalizing of the germ by fertilization' depends the reluctance of nearly all writers to recognise the submitted facts of a continuous and purely parthenogenetic reproduction, as for example in the case of the Ostracoda. It is certainly true that absolute proofs of the indefinite duration of this mode of reproduction cannot be obtained; for unlimited time and innumerable generations are not within the limits of observation; but who doubts whether the sexual method, with which we are so completely familiar, and which is for this reason spoken of as the usual mode of reproduction,—who doubts whether this can endure without limit? And yet this assumption is as incapable of proof by appeal to experience as the other. It appears to be very difficult to get rid of the deeply rooted idea that fertilization is a vitalizing process, a 'rejuvenescence of life,' although we are quite unable to explain the nature of the renewal which is supposed to take place. The old idea of 'vital force' unconsciously bears a part in this view, an idea which certainly does not gain any scientific justification because, as Bunge has rightly said, we are to-day very far from laying bare the deepest roots of any one of the processes of life and explaining it by the operation of known forces. I hardly think that we shall ever reach this point, but until the explanation of vital processes by means of the well-known chemical and physical properties

of matter is proved to be impossible, it will, in my opinion, be unjustifiable for science to relinquish the attempt. The conception of vital force and the conception of fertilization as a renewal of life hang more closely together than we are in the habit of thinking.

The facts of the transmission of hereditary tendencies from both parents to the child, together with the facts of parthenogenesis, induced me, at an early date, to look for the essence of fertilization, neither in the vitalization of the egg, nor in the union of two opposed polar forces, but rather in the fusion of two hereditary tendencies,—in the mingling of the peculiarities of two individuals. The substances which come together in fertilization, from the male and from the female, are not fundamentally different but essentially similar, differing only in points of secondary importance. This is what I meant by the statement, made shortly after the discovery of the fundamental phenomena of fertilization, that the two germ-cells which unite together, are in the proportion of one to one, that is that they are essentially alike.

If this conception be valid, the above-mentioned view as to the extrusion of polar bodies, propounded by Minot, Balfour, and E. van Beneden, must be erroneous; for a male principle such as their theory demands has no existence, and cannot therefore be expelled from the ovum. There is no male or female principle, but only a paternal and maternal substance. If, on the other hand, Minot's Gonoblastid Theory be sound, it follows that my view, which finds the essence of fertilization in the union of the different hereditary tendencies of two individuals, must be abandoned.

It seemed to me possible to settle the question by means of parthenogenesis. If parthenogenetic eggs develope without first expelling polar bodies, then Minot's theory, the 'compensation theory' as O. Hertwig has recently called it, receives material support: if however polar bodies are formed by them, it is impossible that such bodies can represent the male principle of the egg. I succeeded in proving the existence of a polar body, first in the ovum of a parthenogenetic Daphnid, *Polyphemus oculus*, and later, in conjunction with Ischikawa, in the parthenogenetic eggs of various other species of Daphnids, and also in some of the Ostracoda and Rotifera. Blochmann

showed the existence of a polar body in the parthenogenetic ova of the *Aphidae*, and there is now no doubt that polar bodies are formed in most if not in all parthenogenetic eggs. The 'compensation theory' must therefore be given up, and the question arises as to the theory which can take its place.

Before the existence of polar bodies in parthenogenetic ova had been completely established, I had endeavoured to find, in opposition to the 'compensation theory,' another meaning in the polar bodies. The history of our earliest knowledge of the processes of nuclear division, by the work of Auerbach, Bütschli, Flemming, and others, is well known: the existence of most remarkable and excessively minute arrangements for cell-division were shown to exist in the mysterious 'chromatin substance' of the nucleus, the so-called nuclear loops, which are accurately divided in a longitudinal plane, the halves then entering the two daughter nuclei which are being formed. These chromatin rods acquired a new significance when E. van Beneden first showed that they were contained in equal numbers in both the male and female reproductive cells, and that they arrange themselves side by side, to build up the chromatin substance of the embryonic nucleus. Considering this and certain other facts, it became more and more probable that the chromatin rods were the essential factors in fertilization, the substance which was contributed by the parents and fused together in the offspring, and which was therefore, in all probability, the bearer of hereditary tendencies. Strasburger, O. Hertwig, and v. Kölliker also gave expression to this view for which I had contended. We regarded the nuclear loops as that idioplasm which Nägeli had been led, by his acute reasoning, to suggest; a substance which is not fluid, but organized, which possesses an extremely complex structure, and is transmitted from one generation to another.

But this view did not decide the question whether the ovum was not, after all, vitalized by fertilization. O. Hertwig was obviously still under the influence of this idea when in 1885 he maintained in the above-mentioned work, that 'the *fertilizing substance* transmits, at one and the same time, those peculiarities, which children inherit from their parents.' Such an explanation is, in a certain sense, defensible, and we may speak of a 'fertilizing substance,' in so far as the amounts of nuclear material

which unite during fertilization seem to be necessary to determine the commencement of development. But this refers only to the restoration of a certain amount of nuclear substance, rendering its *quantity* sufficient for development, and parthenogenesis shows us that when the second polar body is absent this quantity can be supplied by a single sexual cell. In the precise meaning of the word, as it is ordinarily used, there is no such thing as a fertilizing substance, and the progress in thought from the old to the new doctrine of fertilization can only take place when the idea of such a substance in the old sense is completely abandoned, and when it is recognized that *fertilization has no significance except the union in the single offspring of the hereditary substance from two individuals.*

The advance which has occurred is due to Strasburger's writings as well as my own: the former agreed with O. Hertwig and me as to the essential similarity, as regards their chief constituents, of the two sexual cells, and as to the secondary nature of their differences: Strasburger in fact went so far as to say that all differentiations of sex were simply the means adapted to bring together the two cell-nuclei which were necessary for the sexual act. With this view I not only entirely agreed, but totally rejected the pre-existing dynamic theory of fertilization, in as much as I could not recognize the object of fertilization as the 'vitalization of the germ' or the 'rejuvenescence of vital processes,' but regarded it as simply *the union of the different hereditary tendencies of two individuals.* This union, which has hitherto been regarded, to some extent, as merely a necessary consequence, has become the important feature, while the 'vitalization of the germ' by the interaction of two opposed sexual cells,—formerly looked upon as the essential part of the process,—has declined from this high position and is regarded as only the means by which the process is effected.

I was, at that time, so completely convinced that the facts warranted no other explanation, that I maintained that the nucleus of an ovum might be fertilized as fully by the nucleus of another ovum,—i.e. might be rendered equally capable of development,—as by the nucleus of a spermatozoon. The passage in which I advocated this view runs as follows:—'If it were possible to introduce the female pronucleus of an egg into another egg of the same species, immediately after the transfor-

mation of the nucleus of the latter into the female pronucleus, it is very probable that the two nuclei would conjugate just as if a fertilizing sperm-nucleus had penetrated. If this were so, the direct proof that egg-nucleus and sperm-nucleus are identical would be furnished.'[1] Boveri succeeded in accomplishing this a few years later, although he made use of the nuclei of two spermatozoa instead of those of the ova.

I also hold, in opposition to the rejuvenescence theory, that there is no polar antithesis, and that, in the union which is the essence of fertilization, the nuclear loops contribute neither male nor female principle, but a paternal and maternal substance, and that the significance of fertilization is nothing more nor less than a mingling of the hereditary tendencies of father and mother.

I. The Significance of the Process of Maturation of the Germ-cells.

The Maturation of the Ovum.

Relying on the views set forth above, I have made the attempt to substitute a new explanation of the formation of polar bodies in the animal ovum for that which has hitherto found acceptance. If that substance which is expelled from the ripe ovum in the polar bodies be not the male principle, what can it be?

The cellular nature of the polar bodies has been demonstrated by Giard, Bütschli, and O. Hertwig; van Beneden has shown that they contain chromatin, and that at each of the two divisions which give rise to the two polar bodies, half of the chromatosomes leave the egg in the nucleus of a polar body. If then the chromatin be the idioplasm, the material basis of heredity, or, in other words, that substance which determines the nature and essence of the cell and its descendants, then cells of different kinds must contain correspondingly different varieties of idioplasm. Hence my theory of germ-plasm may be expressed as follows:—The fertilized ovum contains germ-plasm in its nucleus, i. e. idioplasm endowed with the collective hereditary tendencies of the species: at each of the cell-divisions by means of which the ovum developes into the organism, this idioplasm splits into two quantitatively similar

[1] Vol. I. pp. 252, 253.

halves in order to form the nuclei of the daughter-cells. But these halves are not always qualitatively alike; they are only so when they are to give rise to similar cells: when the cells which arise by division have a different significance in development, their idioplasm also differs in quality. *The germ-plasm of the ovum is thus continually undergoing change during ontogeny, inasmuch as the developmental tendencies are being split up, and become more and more distributed among the members of successive cell generations*, until finally each kind of cell in the body contains only that developmental tendency which corresponds with its specific histological character. Each specific cell is thus dominated by a specific idioplasm.

As soon as I had arrived at this conclusion, it was easy and indeed inevitable to refer the differences between spermatozoon and egg-cell to a specific idioplasm which had stamped its peculiarities upon each cell. But since both male and female germ-cells contain the substance which fuses during fertilization to form the segmentation nucleus, and therefore germ-plasm, I concluded that a part of this true germ-plasm which forms the nuclear substance, splits off at the first ontogenetic stage, as specific sperm or egg idioplasm, which controls the germ-cell during its growth, and confers upon it a specific histological character. I sought for the meaning of the cell-division which results in the separation of the polar bodies, in the suggestion that by this means the spermogenetic or ovogenetic idioplasm, rendered superfluous after the attainment of the specific form, was removed from the germ-cell, while the germ-plasm, grown in the mean time to a larger mass, remained behind in the cell. I therefore recognised in the cutting-off of the polar bodies the removal of histogenetic idioplasm from the germ-cells.

While I was busy working out these interpretations, I discovered new facts which caused a modification of this view and led to the conclusion, which up to the present time appears to be sound, that the formation of polar bodies is a *process for the reduction of the hereditary substance.*

The fact which led to this conclusion was the *law of the number of polar bodies*,—the discovery that all animal eggs which require fertilization expel two polar bodies, one after the other, while all true parthenogenetic eggs give rise to one only. Now the ovogenetic idioplasm cannot, at the most, occupy more

than the first polar body; the second must have some other meaning, for if I had been correct in assuming the necessity of the separation of the specific nucleoplasm from the egg, it follows that this substance must be separated as fully and completely from the parthenogenetic as from the sexual egg. The second polar body must therefore possess a different meaning. In the fifth of the essays here collected [1], I first indicated that this meaning is a reduction in the substance which forms the material basis of heredity, in that *the number of the contained ancestral plasms are diminished by one-half* during the halving of the nuclear substance to form the two daughter nuclei. By the term ancestral plasms, I referred to the separate kinds of germ-plasms from different ancestors which, according to my view, must be contained in the germ-plasm of each individual at the present day. If, before the introduction of sexual reproduction, the germ-plasm of each living being contained the developmental tendencies of *one* individual only, its structure would be altered by sexual reproduction; for after fertilization the different germ-plasms from two individuals would meet in the nucleus of the egg; furthermore, the number of these different kinds or units of germ-plasm must necessarily have been doubled with each succeeding generation, so long, at least, as they could have divided, preparatory to fertilization, without relinquishing the power of giving rise, collectively, to the whole organism,—that is, until the units had reached the minimal limits of their mass. From this point onwards sexual reproduction could only have been rendered possible either by a doubling of the nuclear substance, or since this was impossible, by a halving of the germ-plasm of both germ-cells before each act of fertilization, a halving which was not only quantitative, but was above all a separation of the contained individual units, a separation of ancestral germ-plasms, or briefly of ancestral plasms.

Hence, after the discovery of the law of the number of polar bodies, I interpreted the first division of the nucleus as the removal of ovogenetic idioplasm from the egg, and the second as a halving of the number of ancestral units contained in the germ-plasm. Such halving must have occurred, or the number of ancestral units would have been doubled. It necessarily

[1] Vol. I. pp. 257–342.

followed from this view that the ancestral units contained in the spermatozoa must also have undergone a diminution by half. I postulated therefore a reduction of the spermatozoa by division, and, to my mind, there was 'no doubt' that this process occurred in them 'at some time and by some means[1],' although not perhaps in the same manner as in the ova. I even said from the very first[2] that 'it is quite conceivable' that this division might occur in a manner entirely different from that of the egg, since in the former case both daughter-cells might be of similar size and might become spermatozoa, in which case neither of them would shrink and become polar bodies.

The Maturation of the Spermatozoon.

I have not been able to make out, by my own investigations, the facts which confirm the soundness of these views as to the spermatozoa; my impaired eyesight, which has so often put a stop to microscopic investigations, has again rendered the continuation of this research impossible. But Oscar Hertwig[3] has recently given us an account of the development of the spermatozoa of *Ascaris megalocephala*, which not only proves the reduction of the male germ-cells by division, but also shows that it takes place in precisely that way, which from the first I had regarded as most likely.

Since these new facts affect our conclusions with regard to many aspects of the process of fertilization, they are here shortly abstracted. They may possibly enable us to penetrate still more deeply into the meaning and significance of the processes by which the nuclei of germ-cells are reduced in size.

Ever since Edouard van Beneden's classical researches on the process of fertilization, it has been well known that *Ascaris megalocephala* is one of the most favourable objects for the observation of the minute arrangements and changes occurring in the nuclei of germ-cells. The nuclear loops are not only relatively very large, but are also very few in number. Boveri was the first to show that, as regards this number, two varieties of the species exist, one containing two nuclear loops in the young germ-cells, the other containing four. O. Hertwig then

[1] Vol. I, p. 381. [2] Vol. I. p. 385.

[3] O. Hertwig, 'Ueber Ei- und Samenbildung bei Nematoden,' Archiv f. mikr. Anat. 1890.

proved, as might have been expected, that this difference in the number of loops in the youngest germ-cells exists also in the male sex. He called the variety which produces two loops *Var. univalens*, and that which produces four *Var. bivalens*. Since the development of the spermatozoa in both varieties differs only in the number of nuclear loops which are formed, I will,

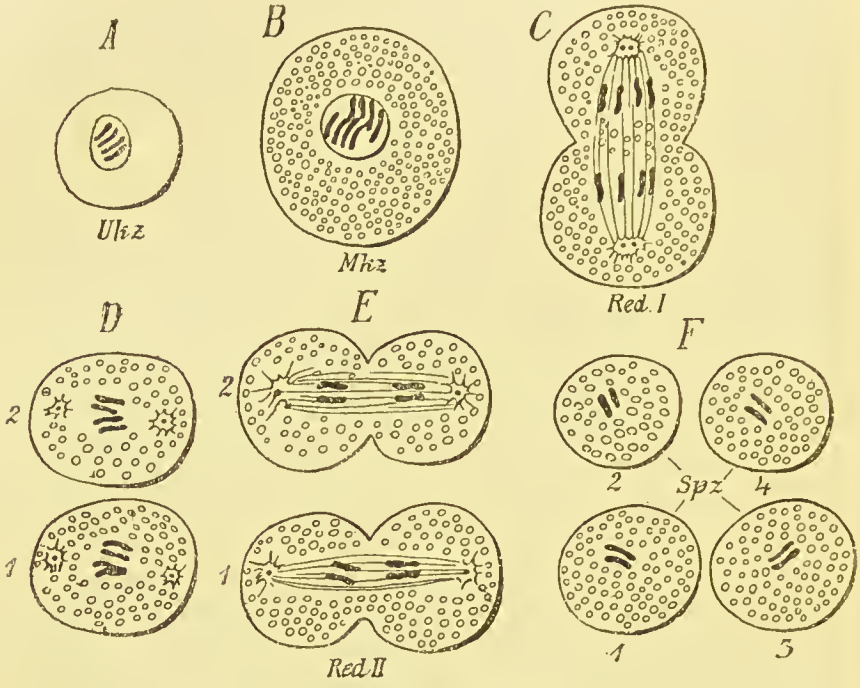


Fig. I.

Formation of spermatozoa in *Ascaris megalocephala*, var. *bivalens* (modified from O. Hertwig). *A*. Primitive sperm-cells. *B*. Sperm-mother-cells. *C*. First 'reducing division.' *D*. The two daughter-cells. *E*. Second 'reducing division.' *F*. The four grand-daughter cells,—the sperm-cells.

in the following account, deal with only one of them, the *Var. bivalens*.

The formation of the spermatozoa falls into three stages; the first is that of the 'primitive sperm-cells': these youngest male germ-cells then proceed to increase by means of successive divisions. The division of the nucleus is effected by karyokinesis after the usual manner; the four nuclear loops split longitudinally and the halves form the two daughter-nuclei. After this process

of multiplication has lasted for a considerable time, the cells pass into the second stage,—that of the 'mother-cells of spermatozoa.' They cease to multiply, grow considerably, and their nuclei pass into the resting condition, viz. the condition of a nuclear network into which the loops break up. When these cells have reached their full size they enter upon the preparation for fresh divisions, which are only two in number and rapidly follow each other. As soon as these are over, the whole development is complete. It is this last stage which brings about the 'reducing division' which I had predicted. The finely divided chromatin bodies contained in the nuclear network build up eight long, thin rods or threads, which afterwards shorten and form thicker rods, arranged by means of the pole-corpuscles or centrosomata, which act in such a manner that four rods are turned toward one pole and four toward the other. A division of the nucleus and of the cell now follows resulting in the formation of two daughter-cells, each of which contains as many nuclear loops as the original sperm-cells, i.e. four. This division is followed immediately by another on the same plan, but without any intervening resting stage: the number of nuclear rods is therefore again halved, so that each daughter-cell of the second order contains but two.

Hence the number of nuclear rods is at first increased from four to eight, and then by two consecutive divisions, this latter number is first halved and then quartered, the final result being *a halving of the number of rods in the original sperm-cells.*

It is well known that precisely the same results are brought about by those divisions of the ovum which give rise to the polar bodies. In the egg the nuclear rods are first doubled and then, by two consecutive divisions, reduced to half their original number. In all essentials, the development of the ovum passes through precisely the same process as that of the spermatozoa. The first two stages, described by O. Hertwig, in the development of the spermatozoa I also find in the formation of the egg. The primitive ova correspond to the primitive sperm-cells, the mother-cell of the ova, or the mature full-sized egg, immediately before reduction by division, corresponds to the mother-cell of the spermatozoa, the only difference being that the egg in this, the second stage, has, as a rule, attained its definite shape and size and is surrounded by its membranes, and that the two last

divisions, which are together spoken of as the 'reducing divisions,' generally take place after the egg has been laid or has, at any rate, left the ovary. This probably explains, as I have already maintained, why the division is so unequal, and why all the daughter-cells cannot become ova, but only the largest of them, viz. that one which alone contains the food-material necessary for the building up of the embryo.

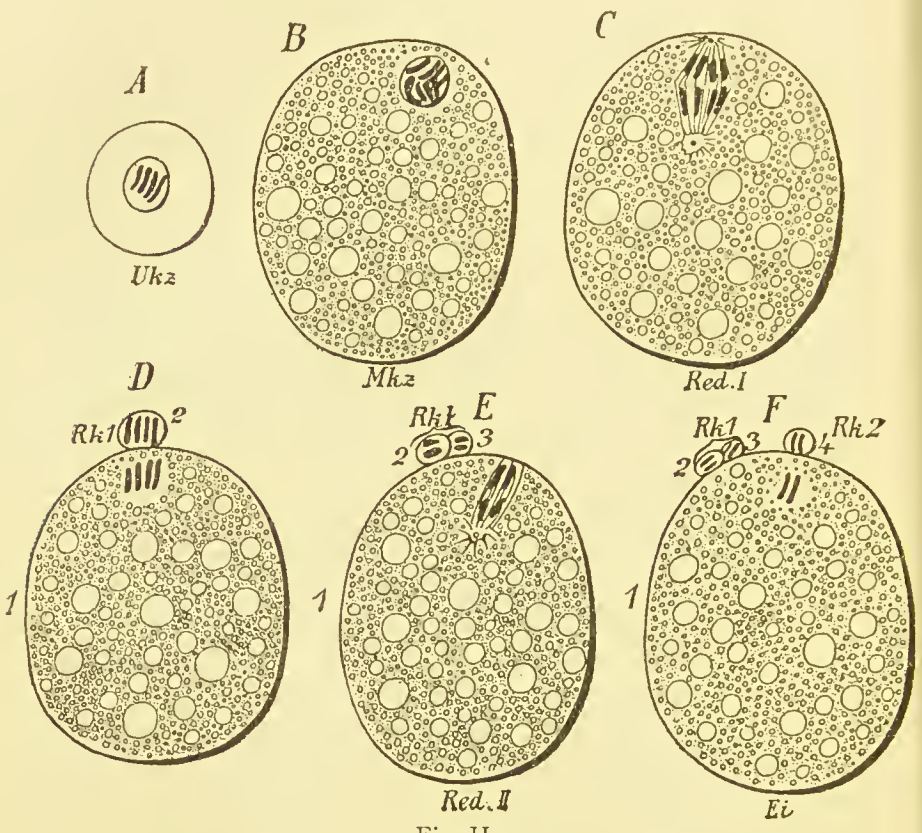


Fig. II.

Formation of ova in *Ascaris megalocephala*, var. *bivalens*.

In other respects the formation of the polar bodies corresponds with the two divisions of the mother-cells of spermatozoa: in both cases there are two successive cell-divisions, and furthermore in the egg both daughter-cells of the first generation divide again—not only the larger one, the ovum, but also the smaller or first polar body—for it is well known that

the latter body generally splits into two secondary polar bodies, and the significance of this apparently aimless division has hitherto been sought in vain. But now we see that it depends on the persistence of a phyletic stage of development, on the survival of an earlier condition, in which the original egg-cells underwent a 'reducing division,' like that of the spermatozoa, producing four cells, each of which was potentially an ovum.

Moreover in another, and obviously a decisive-point, the 'reducing divisions' of ova and spermatozoa are in correspondence; —in the manner and method of the division of the nuclear rods in the daughter-nuclei. The process of karyokinesis here differs from any other mode of nuclear division, in that there is no longitudinal splitting or doubling of the nuclear rods, bringing about a contribution from each rod in the equatorial plate to both daughter-nuclei; instead of this, half the whole number of rods passes to one pole of the nuclear spindle, and half to the other. Furthermore, there is no resting-stage between the two divisions, during which the rods break up into the nuclear network, but the two divisions follow each other without any interval. If the 'reducing division,' for which I have argued, has any existence, we must look for it here; for, so far as proofs can be afforded by observation, they are forthcoming. The number of nuclear rods is reduced to half, and hence the mass of the nuclear substance is certainly halved. And if we must concede that the rods in a nucleus are not absolutely alike, but are derived from the differing germ-plasms of various ancestors (viz. that the rods consist of such different kinds of germ-plasm), it follows that a reduction of the ancestral germ-plasms is admitted.

The new facts discovered by O. Hertwig leave only one point obscure. We see indeed that, in the case of the spermatozoon as in that of the ovum, the nuclear rods are reduced to half, but we ask in vain why two successive divisions are necessary to bring about this reduction, when it seems that a single one would suffice. I had formerly concluded that since parthenogenetic eggs expel only one polar body, instead of the two which separate from all ova requiring fertilization, the first division must have a different significance from the second. I regarded the second division alone as the 'reducing division,' and this was a perfectly sound and logical conclusion, so long as it remained

unknown that the mother-cells of ova contain twice as many nuclear rods as existed in the primitive egg-cells. Until this was known, the 'reducing division' was only required to effect a halving of the nuclear substance, and for this purpose one division would be sufficient. We now know that a second division is rendered necessary because the number of the rods is doubled before the process of reduction has begun. The object served by this doubling remains an obscure point upon which even the spermatogenesis of *Ascaris* does not at present enlighten us. My previous interpretation of the first polar body as the removal of ovogenetic nucleoplasm from the egg must fall to the ground: about this there is no possible doubt, but how can we better explain the necessity for two divisions? Why should the nuclear substance be doubled, only to be halved again? O. Hertwig has also propounded this question, but so far without being able to supply an answer. He hopes that a more accurate study of the manner and method of the arrangement of the chromatin elements in the two successive divisions will ultimately lead to a deeper knowledge of the essence of the whole process of maturation. I also hope the same. The processes which bring about the doubling of the chromatin rods in the resting nuclei of ova and sperm-mother-cells, contain, without doubt, the key to an understanding of the necessity for this increase in number, which at present appears to be so mysterious and superfluous.

Whether unaided observation will ever succeed in making clear the accessory processes, in other words, whether morphological events can be followed in minute detail so far that we can wrest from them the secret of their meaning, we cannot say. Without some guiding idea, it is scarcely possible that the observations of investigators could be directed to the most essential part of the process, especially in this case, where differences of substance are probably present — differences which might be invisible, but are perhaps capable of being inferred by processes of reasoning.

Thus it may be possible, on the basis of Hertwig's observations, to penetrate somewhat deeper into the meaning of the remarkable processes which attend the 'reducing divisions,' if only the subject be attacked from the point of view of the theory of ancestral germ-plasms.

The Double Division of the Nuclear Substance in the Formation of Germ-cells.

With regard to the egg, the following question can be formulated—What is the meaning of the first division in the formation of polar bodies, since the second alone would suffice to halve the nuclear substance? With regard to the sperm-mother-cell however the question must run,—why should division take place twice, when its single occurrence would have sufficed to reduce the nuclear loops by one half? The simplest answer to these two questions is to be found in the fact that the number of nuclear rods is doubled at the beginning of the reducing process, and must therefore be quartered if a diminution to one half the normal number be the ultimate necessity. This leads us to enquire why the preliminary doubling of the nuclear rods is necessary.

Regarding spermatogenesis only, it might be maintained that here we are simply dealing with a process for increasing the number of spermatozoa as far as possible, but if we attempt thus to explain a fourfold instead of a twofold increase, comparison with the egg-mother-cell, producing four descendants of which one only undergoes development, renders any further discussion of this idea superfluous.

In attempting to explain the phenomenon I start from the conception which led me to the idea of a 'reducing division,' i. e. the building up of the germ-plasm, that is the active substance of the nuclear rods, from innumerable ancestral units As I explained on the first statement of this idea, it is a view which is necessarily suggested if we accept certain premisses, the chief of which is, that the hereditary substance from the two parents does not altogether become one during the fusion which occurs at fertilization, but that each retains a certain independence. This agrees with observed facts in so far that, as a result of fertilization, the paternal and maternal rods come to lie close to one another in the same nucleus, but undergo no true fusion into a single mass. If we assume that this remains true during the whole ontogeny, we can only suppose that half the nuclear rods of every cell are paternal and half maternal and that both these simultaneously influence the cell. We do not yet understand how this takes place, and must for the present dis-

miss the question; we do know however that it is an actual fact. We know that the paternal no less than the maternal nuclear rods of the fertilized ovum possess the developmental tendencies of the species, and that either of them alone, that is in the absence of the other, are present in sufficient numbers to regulate the development of the egg, each set containing all that is necessary to originate a mature individual of the species. And the same fact holds good for each successive stage of embryogeny, with just this difference, that the potentiality of stages to come, and not of those passed through, is contained in the embryonic cells. Furthermore every cell contains the separate paternal and maternal nuclear rods, and either set is capable of producing all the subsequent stages. This remains true throughout the whole course of development, from the fertilized ovum which produces the parent, to the male and female germ-cells of the offspring. No real fusion of the two nuclear substances into a single mass ever takes place, so that the corresponding predispositions of the two parents are arranged together, but the hereditary substance contributed by the father remains separate from that contributed by the mother. These substances are made up of units of which each contains those collective predispositions which are indispensable for the building up of an individual, but each possesses an individual character, i. e. they are not entirely alike. I have called such units ancestral plasms, and I conceive that they are contained, in larger or smaller number, in the chromatin of the mature germ-cells of living organisms, viz. that the parental nuclear rods are made up of a certain number of these.

I have thus briefly called to mind the manner in which I conceive that many such ancestral plasms are collected together in a single nuclear mass, and the consequent necessity for a 'reducing division.' It is not perhaps superfluous to return to this subject once more. Each of the parental germ-plasms which, at the phyletic origin of sexual reproduction, for the first time fused together in the segmentation nucleus of the offspring must have contained the potentiality of one individual only, and must have been, in a certain sense, completely homogeneous. Naturally, such a statement by no means excludes the existence of a very complicated structure, in which a number of different predispositions, or of different parts, are collected together, but

it limits each such predisposition to being present only *once*, and *in only one variety*. I conceive of this primitive germ-plasm, as of one single ancestral unit of an existing species, only perhaps relatively larger, its separate predispositions not having been yet reduced to the present minimum.

All this however was altered in the germ-cells of the first sexually produced individual, in which the nuclear rods of the two parents came together, and together composed the hereditary substance of the child. If now, as has been argued above, the paternal and maternal hereditary substances did not fuse but only arranged themselves side by side, there will be found, in the germ-cells of the child, two substances similar as regards the species but dissimilar as regards the individual. If the mass of nuclear substance cannot be increased, both kinds of nuclear substance must be reduced by one half. If we imagine the nuclear material of one such germ-cell to consist of a single thread, one half of it would be made up of paternal and the other half of maternal germ-plasm.

I call to mind the diagram by which, in an earlier essay[1], I endeavoured to make intelligible how the number of ancestral plasms of various kinds which meet together in the germ-plasm are doubled in each successive generation, and how, in the formation of the germ-cells of each generation, the germ-plasms must be reduced to half their size, or their united mass would be doubled in every generation. But in time a limit to this continuous diminution of the ancestral plasms must have been set, and this would occur when the amount of substance necessary to contain all the predispositions of the individual had reached its minimum. Obviously these units cannot become infinitely minute; however small they may be they must always retain a certain size. This follows from the extremely complicated structure which we must without any doubt ascribe to them. These units which make up the germ-plasm of living animals I have called ancestral plasms, but my views about them have been misunderstood, and I have been treated as though I had applied the term to the ultimate biological units of idioplasm. Nothing was further from my mind: I look upon the single ancestral plasms as extremely complex, and built up of countless biological units. I have

[1] Vol. I. p. 369.

retained the conception in its original form, as it is indispensable for the understanding of the 'reducing division.' When I maintained that the units of the germ-plasm are indivisible, I did not refer to mechanical divisibility, but to that division which a unit cannot undergo without losing its original character. If we divide a dog into two parts, neither part is a dog; and so, according to my views, half an ancestral plasm is not an ancestral plasm, is not an hereditary unit capable of calling forth a complete individual; or, to express this with reference to its minute structure, a half would no longer contain all the predispositions necessary for the whole individual. The number of these units would be doubled as the result of each fresh fertilization if the preliminary halving did not occur. Hence the necessity for such halving, which I have attempted to render clear by the foregoing train of thought.

Taking my stand upon this, I argued that a 'reducing division' of the nuclear material takes place before fertilization in both germ-cells,—that is a division contrary to the ordinary method, in that it does not divide the collective ancestral plasms in two equal and similar groups between the daughter-nuclei, as in 'equal divisions[1],' but halves their number so that one daughter nucleus receives one set and the other another set of ancestral plasms. In the ovum I recognised the necessary 'reducing division' in the formation of the second polar body, for it had then been shown by the careful observations of van Beneden and Carnoy upon *Ascaris megalocephala* that two out of the four nuclear rods pass into the second polar body while the other two compose the nucleus of the ovum.

The idea of a 'reducing division,' as I then conceived it, seems to have met with but little acceptance among the German biologists. Except Platner and recently O. Hertwig and Henking, I know of no one who has accepted it. The first-named employed the expression, but without indicating whether he used it in my sense. This cannot be taken for granted, as the simple halving of the chromatin mass may be so designated. All that we can see is a reduction in mass, and the discoveries of Platner and Hertwig do not *directly* teach us more than that in the division of the mother-

[1] For a further account of these methods of division see Vol. I. pp. 369–377.

cell the number of nuclear rods, and therefore the mass of hereditary substance, is reduced to one-half. O. Hertwig appears to accept my views as set forth above: at any rate he thinks that I am 'on the right road in regarding the process by which the second polar body is formed as a reducing process, by means of which an amount of germ-plasm is removed, equal to that which is afterwards conferred by the nucleus of the spermatozoon.' Furthermore, his own account of the significance of the process seems to agree with mine when he says—'In this very simple way it is brought about that the fusion of the two nuclei resulting from the sexual act,—a union of the chromatin substance and the chromatin elements,—does not form double the mass which is normal for the species concerned.'

When, however, we remember that O. Hertwig rejects the theory of ancestral plasms, and takes the antagonistic view of a complete mingling of maternal and paternal germ-plasm, we must be convinced that the reducing process, in the sense in which I have spoken of it, has no existence for Hertwig, and that, from his standpoint, the only conceivable theory is that of a simple reduction of mass. And yet obviously such is not his view, for he speaks of chromatin elements; and hence the question arises as to the kind of elements which these can be if they are not ancestral plasms. It seems to me that the reducing process only acquires a meaning when taken in connection with the supposition of ancestral plasms, unless indeed it is merely a matter of reduction of mass. But it is most improbable that a mere reduction in mass is the object of this very remarkable double division of the nuclear substance, which is never again repeated in the whole developmental history of the animal. First, the mass of nuclear substance is doubled, and then reduced by two divisions to one-half its original bulk. Obviously it would have been simpler if this process had been omitted, and if the nuclear substance of the egg and sperm-mother-cell had, during its growth, merely stopped short at the requisite size. It may perhaps be objected that the growth of the ovum and sperm-mother-cell and their histological structure necessitate such a mass of nuclear substance. We know little or nothing about the relationship of the mass of nuclear matter to the mass of the cell-body, but it must be doubted whether in this case the relation is fixed, because

as a rule ova and spermatozoa differ so enormously in size, and above all because the ova of different species vary so greatly in this respect. Moreover, Boveri has shown us that in one and the same species two otherwise indistinguishable germ-cells exist, one of which contains twice as many nuclear rods as the other, and therefore as far as we can tell twice the amount of nuclear substance. Hence the 'reducing division' cannot be a mere division of mass.

There remain for consideration the 'chromatin elements' of O. Hertwig. What are these elements? Are they the smallest possible portions of living matter, something like the *pangenes* of de Vries? This distinguished botanist in his highly suggestive and thoughtful writings has developed the idea that the nuclear substance of the fertilized ovum is composed of countless very minute particles, called by him pangenes. He thus recalls Darwin's pangenesis, with which his theory has something in common. These pangenes however do not, like the gemmules of Darwin, give rise to cells, but they are the bearers of the various qualities of cells. If we now assume with de Vries that the nuclear substance of germ-cells consists of innumerable kinds of such pangenes, we may regard these either as uniformly mixed together without any kind of arrangement, or as arranged in a definite order. In the first case, each division (reduction) of the mass would only result in a diminution, and the components of both halves would remain the same: the various kinds of 'chromatin elements' would not by this means be reduced to half, but all the elements would be contained in each portion. But if these pangenes were arranged in a regular order in the germ-plasm, and if with Hertwig we designate the groups of these as predispositions, without expressing in any way how such predispositions can be conceived, it follows that a halving of the mass of germ-plasm or nuclear substance would give rise to two halves, neither of which would contain all the predispositions necessary for the construction of an individual, although both might contain many double predispositions. Hertwig imagines that the predispositions which according to his view (loc. cit. p. 110) are present in the germ-plasm of the paternal and maternal germ-cells, mingle together, and de Vries has also assumed this. Hertwig states that 'it is not improbable,' that in the complete union

and mingling of the parent nuclear substances presupposed by him, 'similar predispositions would arrange themselves closer to one another than dissimilar ones, and from the similar but varying paternal and maternal predispositions an *intermediate form* might arise by mutual influence.' I have printed the words 'intermediate form' in italics because it appears that so much depends upon it; for obviously the intermediate form of predisposition must be looked upon as *one* and no longer as two separate predispositions. Hence, according to Hertwig, the fusion of two parental germ-plasms produces an intermediate form of germ-plasm *in which each predisposition is not doubled, but remains single.* Furthermore, this germ-plasm could grow, and could be represented by a larger or smaller mass, but it is impossible that it could be halved without losing its character as germ-plasm, except it were first doubled in size, and all its predispositions were doubled and symmetrically arranged on each side of the plane of division like the antimeres in a bilaterally symmetrical animal. But even in this last case a 'reducing division,' that is a putting on one side of half the number of the corresponding but individually distinct chromatin elements, is impossible because both halves would contain precisely similar predispositions. O. Hertwig deceives himself in believing that he can assume a halving of the number of chromatin elements while his conception of the composition of the germ-plasm only admits of a halving of mass. In his germ-plasm, made by the fusion of paternal and maternal predispositions, there are no differing predispositions of one and the same part or organ: the parental differences have, according to his view, neutralized each other, and each predisposition is present as a single intermediate variety. Whence comes the necessity or the possibility of any reduction? What are the units which are to be reduced in number?

It is clear that we cannot avoid the assumption of higher units of germ-plasm, each one of which *contains, collected together, the varied predispositions of the species*, whether called by my term ancestral plasm, or by any other name. I shall attempt to explain elsewhere that this conception is not only indispensable for our understanding of the 'reducing division,' but that it is even rendered necessary by the phenomena of heredity. At present I do not propose to do more than show that the

idea of a 'reducing division' presupposes the multiplication of the equivalent but individually characterized units in the germ-plasm of the fertilized egg, and that, without this presupposition, the 'reducing division' is entirely devoid of meaning.

If we may now feel greater certainty than ever before in regarding the double division of the egg and sperm-mother-cell as a 'reducing division,' we gain at the same time further proofs that the germ-plasm is composed of ancestral plasms, that is of hereditary units of a higher order, each one of which, if it alone dominated the ovum, would be capable of guiding the whole ontogeny and of producing a complete individual of the species.

Before I attempt to show how these fundamental views throw new light on the discoveries of recent years, I will say a few words on the independence of the maternal and paternal chromatosomes.

According to the views which I have expressed, the nuclear rods are built up of a series of ancestral plasms, which are not intimately connected together, but so far as mere position is concerned, are arranged next to one another. A rod does not represent a kind of 'individuality' (Boveri), by which term there is certainly implied the existence of an internal relationship of parts to one another, according to certain laws, a relationship which prevents any mechanical division of the whole into equivalent parts capable of living and performing their functions. 'Individualities' as defined above are to be found in my ancestral plasms, or as I propose to call them shortly, the '*Ids*'[1]. These cannot be divided without losing the power of building up an individual, while, according to my view, the series of ancestral plasms which compose the rods or '*Idants*'[2] might quite conceivably be removed bodily, by division occurring at any spot, and replaced by others, without any loss of the essential force which controls the ontogeny of the species in question. The only result of such replacement would be to cause a more or less marked alteration in

[1] The expressions *Id* and *Idant* serve to recall Nägeli's 'idioplasm,' from which they are derived. I think it is very necessary to substitute some short expressions for the clumsy 'ancestral plasms' and 'chromatosomes,' or the frequently inappropriate 'nuclear rods' and 'nuclear loops.'

[2] See the preceding note.

the individuality of the being which is produced by this ontogeny.

There is therefore, in my opinion, nothing inadmissible in the idea of the breaking up of the chromatin rods or idants, during each nuclear resting stage, if only the single ids remain unchanged; but certain facts in heredity, to be mentioned immediately, support the view that the specific hereditary substance from one or both parents can be contained in the germ-cells of the child, and this presupposes that it is at least possible and perhaps the rule, for the order and arrangement of the ids in the idants to remain unchanged from the germ-cells of the parent to those of the offspring. I would, then, assume that, at least on the way from germ-cell to germ-cell, the views of van Beneden and Boveri are upon the whole correct, viz. that the chromatosomes (idants) only apparently break up during the nuclear resting stage, but in reality persist. I imagine that, after the period of the resting stage, they are generally composed of the same ids, for the most part arranged in series similar to those which existed before the preceding nuclear division. We are already acquainted with such astonishingly delicate mechanical arrangements in cells, that the existence of special provision for maintaining the original arrangement of the rod elements (ids) might be looked upon as very far from an impossibility. Even if direct observation should fail to answer this question in the future, some certainty might be reached by those indirect means which often lead us to a final decision in such excessively minute biological questions—viz. the means provided by an examination of the facts of heredity. Even now there is, I think, one such fact, supporting the idea of a continuity of the idants; I mean the frequently observed fact that a child may predominantly or even exclusively resemble one of its parents alone. If the elements of the chromatin rods, i. e. the ancestral plasms, were irregularly mingled together in each nuclear resting stage, to be rearranged at random in the idants, it would scarcely ever happen that the scattered ids would come together in a series like that which existed in the original paternal or maternal idants. The individual stamp of a nuclear rod (idant) must entirely depend upon its construction out of particular ids. Nevertheless, we must not regard this constitution as for ever unchangeable. The universally observed change of indivi-

duality which takes place in the course of generations, and the fact that one and the same individuality is never twice repeated, suggest to my mind an occasional change in the arrangement of ids within the idants—a change which, if it does not occur at every opportunity afforded by reconstruction, will at any rate take place in the course of generations.

I will not now enter more fully into the foundation of such protracted, and, to a certain extent, secular changes of the idants, but will turn at once to the problem propounded above as to the meaning and significance of the fact, which has been firmly established by the researches of O. Hertwig upon *Ascaris*, that a double division of nucleus and cell is rendered necessary by that reduction of idioplasmic elements which is required by my theory in both ovum and sperm-cell; in other words, *to explain the fact that the number of idants is doubled before being halved.*

Inasmuch as two primary polar bodies are formed, so far as we know, by all eggs which require fertilization, we may conclude that the significance of the double division of the sperm-mother-cell of *Ascaris megalocephala* is typical and far-reaching, rather than merely accessory or secondary.

If, as I have shown above, the significance of the original increase of the chromatin rods to double their number does not lie in the needs of the growing ovum or spermatozoon, it must be sought for in some other direction. *It lies, as I believe, in the attempt to bring about as intimate a mixture as possible of the hereditary units of both father and mother*[1].

If the first object of sexual reproduction is to combine the hereditary tendencies of two individuals, and not in a mere transitory manner (viz. in the single individual proceeding from one act of fertilization), but permanently, because such a combination affects also the germ-cells of each single individual, and therefore of all succeeding generations,—if this be its object, then we must admit that it is mechanically possible for a combination of paternal and maternal idants to exist side by side in the mature germ-cells of the individual. This is obviously conceded if the 'reducing division' makes

[1] Histologists may perhaps object that the doubling of the idants simply depends upon a postponement of the normal longitudinal fission until the time at which the spindle is formed. This is probably correct, but it only explains the existence of the doubling and not its significance.

no difference between the maternal and paternal nuclear rods, but leads to a halving of their number in such a manner that the most varied combinations can arise; so that if $a+b$, and $c+d$ represent four rods, there will be found in the mature germ-cell not only the paternal group $a+b$ and the maternal $c+d$, but also the combination $a+c$ and $b+d$ or $a+d$ and $b+c$, that is combinations of any paternal with any maternal element.

Now it is clear that only very few distinct combinations can be brought about in this way,—in the above-mentioned case of four rods, only six combinations. But if, as actually happens, each of the rods is doubled before their number is halved, there are a greater number of possible combinations, viz. in the above case, ten. Hence an individual of such a species could produce ten kinds of eggs or spermatozoa with differing hereditary tendencies. At the fertilization of one of these eggs by a spermatozoon of another individual of the same species, two different idants would meet each other. Each parent produces ten different kinds of germ-cells, hence as many different children can proceed from such a union, as there are possible combinations between the ten kinds of spermatozoa of the father and the ten kinds of ova of the mother, namely ten times ten or a hundred. I therefore believe that *the significance of the longitudinal splitting of the idants, and the consequent doubling of their number, is an increase in the number of possible combinations.*

It may be doubted whether the increase which is thus rendered possible is sufficient to explain certain phenomena of heredity. So far as our knowledge extends, it has never happened that two children of the same family born successively have had that resemblance to each other which is familiar in the case of identical twins. Precisely similar germ-plasm never seems to be twice formed in the unions of the same parents; it only occurs in those exceptional cases in which a fertilized ovum produces two children, when the germ-plasm which gives to both of them proceeds from a single egg and a single spermatozoon. Now a hundred different combinations of germ-plasms can occur under the given conditions, while a human pair can scarcely produce more than thirty children: but if only ten were born, one of the hundred

possible combinations might repeat itself. From this point of view, it might therefore be doubted whether the doubling of the idants in the germ-mother-cells, together with the succeeding two 'reducing divisions,' are sufficient to explain the fact that identical children only appear in the form of twins developed from a single ovum.

It may however be urged that the assumption of only four idants may not hold for the human species, and that in such animals as *Ascaris megalocephala bivalens*, which undoubtedly possess only four idants, we cannot appreciate the phenomena of heredity when applied to the minutest individual differences, as we can in the case of man. It is quite conceivable that many fertilized ova of this species of *Ascaris* contain precisely the same kind of germ-plasm, that is the same combination of ids; we do not however know that this is the case. We are unfortunately ignorant of the number of idants which is typical for man, and can only assert that it is probably higher than four. But the number of possible combinations increases very rapidly with an increase in the number of idants. Certain Mollusca, as *Carinaria* and *Phyllirhoë*, possess thirty-two idants, and in Crustacea the number is even higher. Eight idants, without doubling, would render possible seventy combinations, doubled, they would produce 266: similarly, without and with doubling twelve idants would yield 924 and 8074 combinations respectively; sixteen would yield 12,870 and 258,570; twenty would yield 184,756 and 8,533,606. With thirty-two idants doubling increases the number of combinations about 500 fold[1].

If we now remember that an equal number of idants from each parent meet together during fertilization, and that each of the parental groups of idants represents only one of the numerous combinations which are possible for the species, it is evident that the number of possible variations of germ-plasm which a single pair is capable of producing must be extremely great, for it is a number obtained by multiplying together the maternal and paternal number of combinations. Thus twelve idants yield 8074 × 8074 variations. Although even this large number of combinations does not exclude the

[1] For these figures I am indebted to the kindness of my mathematical friend, Professor Lüroth of Freiburg im Breisgau.

possibility of a repetition (two or more times) of the same combination, and the further possibility of the development of those very germ-cells which contain identical germ-plasm—the probability of such an occurrence is so excessively remote that it may be considered practically non-existent, and we have no reason for wondering that identical individuals have never been observed among the children successively born in any human family.

To my mind the doubling of the idants before the 'reducing division' possesses this very significance:—it renders possible an almost infinite number of different kinds of germ-plasm, so that every individual must be different from all the rest. And the meaning of this endless variety is to afford the material for the operation of natural selection.

It might perhaps be objected that sufficient variety could have been attained without the doubling of the rods, and that, although the difference between the numbers of combinations produced with and without doubling is certainly very considerable, the number of rods would have been large enough without increase, since, as a matter of fact, the number of descendants developed is always smaller than the number of possible combinations. Eight idants without doubling give seventy combinations; these multiplied by the seventy combinations of the other parent yield 4900 varieties of germ-plasm in the fertilized ova, and potentially an equal number of different offspring. We might suppose that this number would suffice in all cases; for when the germ-cells are far more numerous (many animals producing 100,000 or even upwards of 1,000,000 ova, not to mention spermatozoa) only a very small percentage can enter upon development, and of these but very few can arrive at maturity and reproduce themselves. It would be sufficient, we might think, if there were only a few more thousand combinations of germ-plasm than of individuals which attain maturity.

There is, however, much to be said on the other side. If we are not able to determine by calculation the number of differing individuals which are necessary in order that the development of the species may be guided by natural selection, we can scarcely fail to recognize that it is only by the widest possible choice that the best possible adaptation of

all parts and organs can be ensured in every case. The extraordinary superfluity of individuals in each generation is indispensable for that intense selective process which must have operated without ceasing if it is to afford the explanation of universal adaptation. And if among the thousands of germs, which sooner or later succumb in the struggle for existence, there were always a hundred which contained the same combination of individual characters, *it is clear that this number would not count for more than one, as material for natural selection.* It is just because each fertilized germ, and the individual arising from it, are different from others as regards the combination of characters, that the completeness of adaptation is rendered possible. It follows from this arrangement that the highest possible number of combinations of germ-plasm are offered for the operation of natural selection.

It must furthermore be borne in mind that the full number of possible combinations, which is mathematically calculable, is, in practice, very far from being attained. We must assume in the calculation that the nuclear rods possess a limitless power of combination; but this is neither proved, nor is it probable. We are on the safe side in assuming that certain combinations are formed more readily than others, and are for this reason of more frequent occurrence. And it must not be forgotten that identical ancestral units (ids) and identical idants may be present in the germ-plasm. Widely different ids are not contained in every individual of a species, and perhaps never occur in the same individual. In many cases the two parents are in some degree blood relations, and would contain similar or similarly composed idants. Although direct observation can tell us nothing on this point, it can still be shown that identical idants may be found in one and the same nucleus. This is proved by the doubling of the rods which takes place before the 'reducing division,' and it can be inferred with equal certainty from other conditions.

The two idants which arise in the mother-cell of the ovum, by the longitudinal splitting of a single one, must contain similar combinations of ancestral units. If this were not so, it would follow that each of the two daughter nuclear rods would contain different ids, and hence the number of ids in each single idant would necessarily be diminished by half. But this cannot be

the case, or the two successive 'reducing divisions' would lessen the total number of ids, in each germ-cell, to one quarter. Two idants are the normal number in *Ascaris m. univalens*, and they are increased to four, by longitudinal fission : a single idant is contained in each mature spermatozoon or ovum which is formed by the two successive 'reducing divisions.' Hence

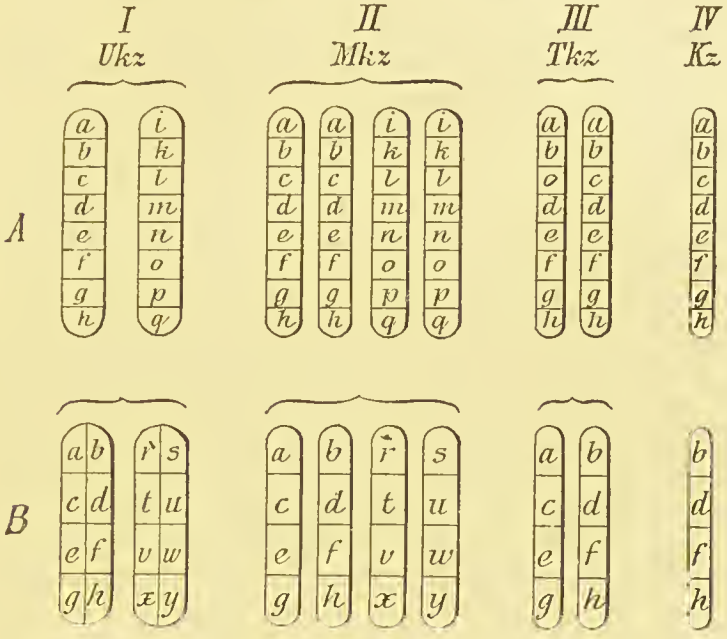


FIG. III.

Diagram showing the behaviour of the idants in the various stages of the development of the germ-cells in *Ascaris megalocephala*, var. *univalens*. *A* shows the actual behaviour of the idants, the final result (*IV*) of which is a halving of the number of ids present in the first stage (*I*). *B* shows that the arrangement of ids as a double row within the idants would cause the final number (*IV*) to be a quarter of that present in the first stage (*I*). Each of the four groups of figures in both *A* and *B* represents the idants of a single cell of the corresponding stage.

these mature germ-cells must contain half the total number of ids contained in the two idants of the original germ-cell. If this be so it is clear that the ids in the mother-idants are doubled in number by longitudinal fission. The small letters *a*, *b*, *c*, &c. in the diagrammatic figure III, represent the ids which compose the idants. The numbers *I–IV.* represent the idants of each of the four stages,—the primitive germ-cells,

the mother-cells of the first and second order, and the germ-cells. The series *A* represents eight ids in each of the two idants of a primitive germ-cell, arranged as a single row; whereas in series *B* they form two rows. In *A* the idants of stage *I* give rise, by longitudinal fission, to the four idants of stage *II*, *that is to two pairs of identical idants*: in series *B* the two original idants similarly produce the four idants of stage *II*, each of which is different from the others and contains only four ids. In consequence of this, in series *B*, the two successive 'reducing divisions' diminish the total number of ids in the cell, first (stage *III*) from 16 to 8, and then (stage *IV*) from 8 to 4—i. e. to one quarter the normal number of ids; in series *A*, on the other hand, the corresponding divisions lead to that halving of the normal number of ids which is in accordance with theory—i. e. from the 16 of stage *I* to the 8 of stage *IV*.

It should be regarded as certain that many identical ancestral units may be present in the germ-plasm of a germ-cell, and that identical nuclear rods may exist side by side. Furthermore, during fertilization, as has been mentioned above, identical nuclear rods from the two parents must meet together, the frequency of this depending upon the amount of interbreeding (using the term in its widest sense) that has occurred, or in other words upon the limit set to the number of individuals in any given area, and upon the restriction in the number of ancestors of the species. Such considerations enable us to understand why nature has provided such superabundant variations in the germ-plasm of the reproductive cells of a single individual. It is the same with the more obvious prodigality that she lavishes in the millions of germ-cells brought forth by every individual *Ascaris* or sturgeon. We now know that this apparent waste is necessary in order to ensure that, on the average, at least one or two germs may reach maturity, and that thus the species may be maintained.

Other Types of Maturation of Germ-Cells.

I would here repeat that, before O. Hertwig, Platner had shown that an entirely similar process occurs in the double 'reducing division' of the mother-cells of the spermatozoon in both the butterfly and the snail. He observed the original

doubling of the idants (chromatosomes) and their subsequent reduction to half. Furthermore, the observations of Flemming on the formation of spermatozoa in the salamander prove that there is an initial increase of the nuclear loops to double the normal number. These facts enable us to recognize a relationship, which Hertwig has already propounded in his account of the type of 'reducing division' met with in *Ascaris*. Platner had previously recognized the homology between the formation of spermatozoa and of ova, between the two divisions of the sperm-mother-cell and the formation of the two polar bodies. Inasmuch as these homologies have been proved to exist in a worm, in insects, and in a vertebrate, and since also that double division which leads to the extrusion of the two primary polar bodies is certainly a character common to the Metazoa, we may well believe that we are dealing with a process of general significance, and one which is repeated during the formation of the sexual cells of, at any rate, all the higher Metazoa, in essentially the same way.

Hence, after writing the remarks which appear above, I was much astonished by Henking's pamphlet on the formation of ova and spermatozoa in an insect, *Pyrrhocoris apterus*, in which the process is described as following an entirely different plan. The observations are clearly exact and trustworthy, and if the author's explanation be valid, it is impossible to attach to the processes of maturation in this insect a meaning similar to that found in the other animals which have been studied. I believe, however, that Henking's interpretation is erroneous on one point, and that the apparently profound differences can be reconciled, in fact that they are beautifully adapted to make clear the essential parts of the process.

The difference between the formation of spermatozoa in *Pyrrhocoris* and *Ascaris* depends upon the fact that, in the former, there is no doubling of the idants before the first division of the sperm-mother-cell, yet the first division takes place as it does in *Ascaris*, so that the existing number (24) of idants is halved, twelve passing to each daughter-nucleus. The latter then enters upon the second division in the usual manner, each of the twelve idants splitting longitudinally, and their halves passing into the grand-daughter-nuclei. These last grand-daughter-cells constitute the sperm-cells, and the final result of

the process is the same as in other cases; for the mature germ-cells contain only half the number of idants which are normally found in the species.

Henking interprets his corresponding observations upon the development of the ova, in the following manner:—The first division of the mother-cell is the 'reducing division' suggested by me, for this alone reduces the idants to half their normal number: the second division is that which I have called the 'equal division,' i. e. the means by which a number of ids, equal to that present before this division commences, passes into each daughter-nucleus; and this is rendered possible because the longitudinal splitting of the idants depends upon a doubling of the ids by division.

If this explanation be valid, the interpretation offered above of the doubling of the idants in the mother-cells of *Ascaris* must fail, and I doubt whether any other feasible explanation is to be found. Henking attempts to reconcile the discrepancy between the two observations by altogether doubting the doubling of the nuclear rods of *Ascaris*. I have, however, convinced myself, by an examination of the preparations of my pupil, Herr Arnold Spuler, that the doubling cannot be denied. Furthermore, it was this very process which first afforded an explanation of the double division of the mother-cells. Why then should there be this universal double division of which we are so completely assured by the general occurrence of the two polar bodies of the ovum? Regarding spermatogenesis only, we might perhaps be inclined to be satisfied with the answer that the number of sperm-cells must be four times that of the mother-cells. But, as I have indicated above, the mere increase of the spermatozoa might be brought about, and to any extent, by additional division of the original sperm-cells; and when we remember that the mother-cell of the ovum undergoes this double division, whereby three out of the four daughter-cells simply disappear as polar bodies, it becomes clear that the process is controlled by some deeper necessity. And if anyone doubts this, and is inclined to think, with Lameere and Boveri, that the polar bodies are merely a phyletic reminiscence, he should remember that rudimentary organs and processes always tend to vary, and that it is inconceivable that, in all sexually reproduced Metazoa, these two nuclear divisions

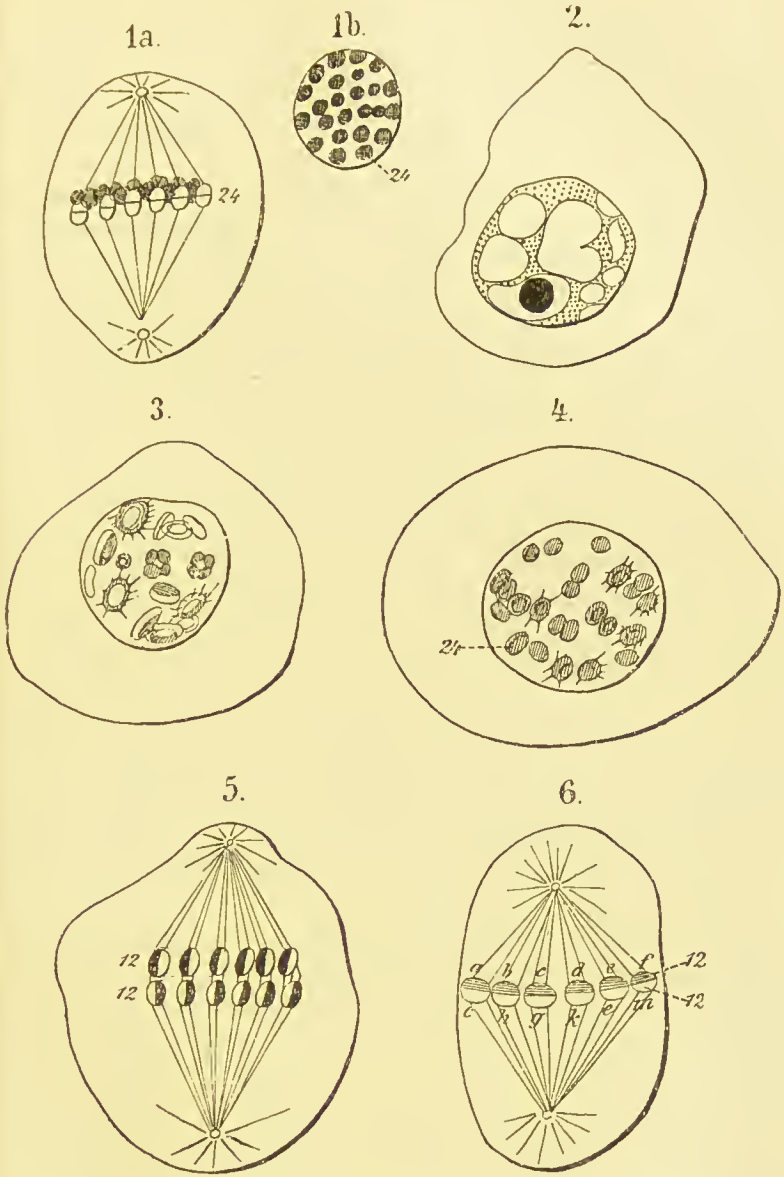


FIG. IV.

Formation of spermatozoa in *Pyrrhocoris* (modified from Henking). 1. Primitive sperm-cell containing nuclear spindle preparatory to division : a. The equatorial plate as seen from the side, b. as seen from above. 2. Sperm-mother-cell. 3. Sperm-mother-cell preparatory to the 'reducing division.' 4. The same, after division of the chromatin-wreaths into 24 double idants. 5. First 'reducing division.' 6. Second 'reducing division.'

should have been retained if obsolete, *and should have shrunk to only one, as soon as regular parthenogenesis commenced.*

The double division must have some meaning, and one which is the same in the formation of both spermatozoa and ova.

I accept the meaning which has been indicated above, and believe that Henking's observations can be easily brought into accord with the plan of formation of sexual cells observed in other species. Henking looks upon the first division of the mother-cell as a 'reducing division,' the second as an 'equal division,' and considers that he uses these terms in the sense in which I have employed them. But this is not quite the case. I understand by a 'reducing division,' one in which the number of ids present in the passive nucleus is reduced to half in each of the daughter-nuclei: I understand by an 'equal division' one in which each daughter-nucleus is provided with the full number of ids present in the passive nucleus of the mother-cell. In the latter case, the daughter-nuclei will contain similar ids, but, in the former, this can only occur when the ids of the mother-cell are precisely identical. I have never maintained that these two contrasted modes of division must be invariably recognizable and distinguishable by external characters, and I have never identified the chromatosomes of authors with my ancestral units. But only when such an identification is assumed does the reduction of the number of ids by one-half (i.e. a 'reducing division' in my sense of the term) necessarily imply a reduction in the number of chromatosomes as well. The types of 'reducing' and 'equal divisions,' as I propounded them in 1887[1], are so conceived that the first involves a halving of the number of idants, while the second does not. But I expressly added—'I do not mean to imply that it is impossible to imagine any other form in which they [viz. these modes of division] may occur[2].' It then seemed to me that the form of nuclear division which is accompanied by a longitudinal splitting of the idants arranged in the equatorial plate of the spindle, can scarcely be conceived of as other than an 'equal division,' but even then I added the words 'as far as I can see[3].' If we assume the linear arrangement of ids in a single row in

[1] See Vol. I. pp. 366–379, and especially pp. 375–377.
[2] See Vol. I. p. 375.
[3] See Vol. I. p. 375.

the idant, the longitudinal splitting of the latter certainly involves an 'equal division.' It appears doubtful, however, whether this arrangement is universally present, and I should be inclined to question its existence in the second division of the mother-cells of *Pyrrhocoris*, and to believe, on the other hand, *that the ids are arranged in two rows, and that the idant is in reality double.* This arrangement would then lead to a new and different type of 'reducing division.' If the letters *a b c*, &c.—*m*. in Fig. V, represent the ids, and the vertical line drawn through *A*, the plane of splitting, it is clear that division of the idant would result in a reduction of the total number of ids to half in each of the daughter-nuclei, as is shown in *B*.

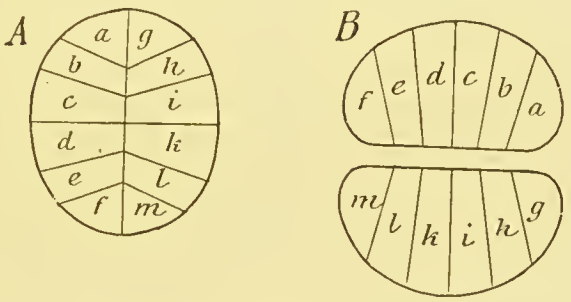


FIG. V.

A. One of the double idants from the equatorial plate of the nuclear spindle of the first 'reducing division.' *B*. The same, showing its position after the occurrence of the first 'reducing division' in the equatorial plate of the nuclear spindle of the second 'reducing division.' (Compare Fig. IV. 5 and 6.)

In support of this assumption there is not only the impossibility of conceiving the universal occurrence of a second division which is not also an *essential* change in the nuclear substance, but, as will be afterwards shown, there is in addition the evidence derived from the figures of the process which Henking has published.

The equatorial plate of the nuclear spindle of the first 'reducing division' is composed of two sets of twelve idants arranged in two wreaths opposite to each other (see Fig. IV. 5). Twelve then pass to one and twelve to the other pole, completing the first 'reducing division.' Now it can be clearly seen that each idant is *double* from the *very first*, consisting of two halves which are arranged side by side in the spindle

of the first 'reducing division' (see Fig. IV. 5). In the second 'reducing division' they are twisted so that the two halves of each idant come to lie upon each other, and between them passes the plane of division which confers upon each daughter nucleus its predetermined half (Fig. IV. 6). If then, these two halves, which are prepared so early, contain similar ids, we have to do with an 'equal division'; but, in my opinion, there is little to be said in favour of this assumption and much for the contrary.

If we enquire as to the origin of the double idants in the equatorial plate of the first 'reducing division,' we find that deeply staining strands and granules of chromatin separate out from the passive nucleus of the mother-cell (Fig. IV. 2) and arrange themselves in the very remarkable likeness of a series of wreaths[1] (Fig. IV. 3), of which there appear to be twelve. The full number may not be visible at the same time, because one or more is as yet incomplete or is already broken up. Each wreath then divides into two similar halves, which by contracting become spheres and give rise to the twenty-four spherical idants in the equatorial plate of the first 'reducing division' (Fig. IV. 4 and 5). There is, indeed, good cause for regarding a process of so definite a character as by no means devoid of meaning, and we naturally ask for the significance of this wreath-formation. We cannot expect to find the answer by direct observation alone, but when we seek assistance from the suggestive conception of the idioplasm, as built up of ids, a certain meaning is seen to underlie the process.

During the resting-stage the ids are scattered through the nucleus; they then collect together again into idants, as I assume, in an order nearly the same as that previously taken; the idants then grow *and double themselves* without any separation of the halves from each other (Fig. VI. 1).

These double idants unite together in pairs, forming wreaths (Fig. VI. 2 and 3), and each of the latter divides into two similar halves (Fig. VI. 4), giving rise to two new double idants (Fig. VI. 5), which may be different from those of the original pair. For the adjoining Fig. VII shows that according to the position of

[1] The term 'wreath' or 'rosette' is sometimes given to the equatorial plate of Flemming (see Klein 'Atlas of Histology,' p. 442). This is of course entirely different from the wreaths mentioned above.—E.B.P.

the plane of division ($x-x$) the halves of the wreaths may be built up of different combinations of ids.

Hence, according to this hypothesis, in the first 'reducing division,' we find in the equatorial plate of the nuclear spindle, twenty-four double idants, the halves of which lie over each other in two rows (Fig. IV. 5), and, which separating into single idants, bring about the second 'reducing division' (Fig. IV. 6).

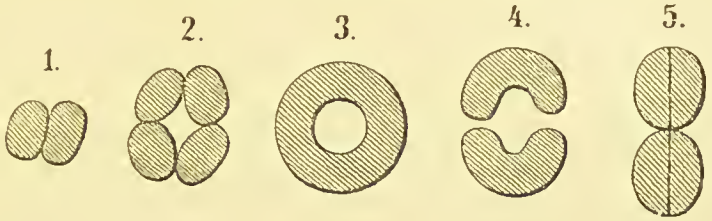


FIG. VI.

Formation of double idants in *Pyrrhocoris*.

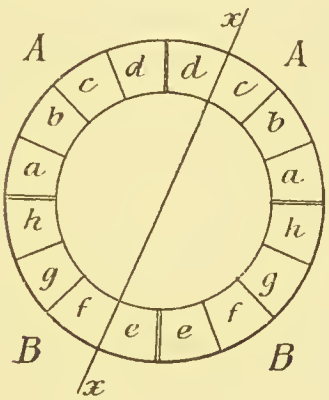


FIG. VII.

A wreath, formed of the four idants *A*, *A*, *B*, *B*, about to divide, through the moveable plane *x*—*x*, into two double idants. The small letters denote the ids, of which only four are shown in each idant.

For some years I have imagined to myself the grouping of the ids into idants, by the arrangement of the former in the figure of a wreath, a form which renders possible a moveable plane of division. It would seem that this arrangement actually obtains in the 'reducing division,' and that nature produces a form which I had only conceived as a diagram.

The formation of wreaths by the idioplasm, during the

'reducing division' of the germ-cells, is not confined to *Pyrrhocoris*; for Flemming long ago described an entirely similar ring-like structure in the salamander, and my assistant, Dr. Häcker, has recently observed the formation of wreaths of idioplasm in the egg-mother-cells of certain Copepoda. The development of these latter does not, however, altogether agree with that of the wreaths of *Pyrrhocoris*, although the same purpose is served—viz. the arrangement of the ids in fresh groups.

Objections.

The objection may be raised to my interpretation of the processes of maturation in *Ascaris*, that, although it corresponds sufficiently well with the variety *bivalens* and with all other animals possessing four or more idants, it does not apply to those with only two, such as the variety *univalens*. When the mother-cells contain only two idants, the mature germ-cells contain only *one*, and hence it is a matter of indifference whether the 'reducing divisions' are preceded by the doubling of the idants or not. It might be maintained that this doubling and the consequent necessity for two divisions, are not explained by my interpretation.

For this variety of *Ascaris megalocephala*, the objection is certainly valid; but the question arises whether this is by itself sufficient to undermine the whole attempt at explanation.

In the first place, in no other living being have so small a number of idants been found as in this variety of *Ascaris megalocephala*. Even so few as four idants occur but rarely; and in the nearest relatives of the species, for instance in *Ascaris lumbricoides*, twelve idants are found; in other Nematodes, according to Carnoy, there are eight to sixteen; in *Sagitta*, according to Boveri, eighteen; and the same number in *Echinus*; in a Medusa, *Tiara*, twenty-eight; and in three different genera of molluscs thirty-two. *Ascaris m. univalens* is in this respect an exception, and should perhaps be dealt with from this point of view, especially as the variety *bivalens*, with four idants, appears to be the more common. We know nothing about the phenomena of heredity in this parasite of the horse, and cannot decide whether the descendants of the variety *bivalens* are not

perhaps a really different species from those of the variety *univalens*. In any case *bivalens* would be the ancestral form.

While studying the last of O. Hertwig's works, the thought occurred to me whether the fresh combination of ids in *Ascaris univalens* might not be brought about in a manner different from that of the simple rearrangement of idants, and I will take this opportunity of expressing the idea, in order that its accuracy may be tested by the facts. The material for such proof or disproof is not at present accessible to me; for the variety *univalens* does not seem to occur in south-west Germany.

In the sperm-mother-cells of *Ascaris m. univalens* four long thin threads are formed from the chromatin distributed in the nuclear network of the resting-stage; these threads are arranged so that they cross each other at one point and are there joined together by means of a connecting cement-substance ('Linin'). Thus they form an Ophiurid-like figure in which the body of the Echinoderm represents the place where crossing occurs, while the paired arms represent the halves of threads. According to O. Hertwig, each of the threads then gradually shortens itself until at length it resembles a short thick rod. The four rods arrange themselves in two pairs, all four bases being closely apposed, the spindle of the first 'reducing division' is formed, and finally each daughter-nucleus receives one of the pairs.

Naturally, O. Hertwig was unable to follow these processes directly, but he inferred them by combining the very numerous stages observed. I should be inclined to look for a somewhat different interpretation of the figures given by him, and would ask whether the four threads which take the form of an Ophiurid, are converted into the rods, not merely by shortening, but by the simultaneous *fusion of two half threads* just as if the paired arms of the Ophiurid, which lie side by side, were to grow together. Many details support this view. First, the connecting cement-substance at the point where the threads cross certainly possesses some significance. If, however, the nuclear rods arise by the shortening of the long threads only, it would appear to have no meaning. Only if we consider that it arises from the coupling together of different halves of threads, would it possess a meaning, as will be immediately seen. If the

halves of threads, representing the arms of the Ophiurid, are directed to each other by the activity of the achromatin nuclear network as they are moved hither and thither, it is essential for them to have a central point of support, i. e. the part representing the body of the Ophiurid. No conclusive objection can be raised against the view that the shortening process is by itself sufficient to convert a long thread into a short thick rod; for we know that nuclear threads are subject to great shortening. But Hertwig himself seems to have had some doubts as to the validity of this explanation which he offers. In support of it he reminds us of 'the considerable shortening undergone by the threads in the spermatozoa of the salamander,' but he adds that this amount is very far below that required in the case of *Ascaris* if his interpretation is to be accepted.

The bifid form of the rods indicates the longitudinal fusion of two threads with their points left free, and finally the position of the rods with their bases apposed, and thus standing as it were, back to back, is more intelligible when we suppose that adjacent arms of the Ophiurid are fused together, rather than that each of the long chromatin threads has shortened to a rod. If the latter were true we should expect that the rods would lie in the middle of the mass of 'linin' representing the Ophiurid body[1], and this, according to Hertwig's figures, does not seem to be the case.

We may very properly be asked for the observations which support this view of a fusion between the halves of threads. So careful an observer as O. Hertwig can scarcely have overlooked these stages, if they have any existence. This I freely acknowledge; but in Plate I he shows a series of figures in which two arms of the Ophiurid are approaching each other, and are more or less fused together. Perhaps Figs. 27, 28, 29 should be understood in this way, and we might then conclude that the threads only begin to fuse after they have already undergone considerable shortening, and further that the fusion commences at the position of crossing and proceeds

[1] Because the middle of each long thread passes through the centre of the 'linin,' while the gradual shortening of the two ends would finally reduce the thread to this greatly thickened middle part. If adjacent halves fused together there would be no such arrangement: they would tend to radiate away from the mass of 'linin' in which their bases alone would lie.

towards the ends, so that at last only the two points are left free. Of course all this can only be tested by the preparations themselves, and O. Hertwig is in the best position, from the great number of his sections, to decide whether his interpretation or that which I have offered, is the right one.

Should my surmise be confirmed, it follows that even in so small a number of idants as exist in the variety *univalens*, a number of combinations would be possible, inasmuch as halving the rods doubles the number of units capable of combination, and, of course, any two half rods might fuse in the manner described above.

It would be very easy to explain the fresh combinations of germ-plasm in all species, *Ascaris m. univalens* included, if we might assume that the idants were freshly built up of irregularly distributed ids after each resting-stage of the nucleus. But the above-mentioned facts concerning hereditary transmission from one parent alone, which have already been used as evidence, are opposed to this view.

It is self-evident that I am far from claiming to have found the correct interpretation of the details in every case. When other workers have tested anew the processes with which my attempted explanation deals, and when new facts have been discovered, we shall gradually arrive at greater certainty. I chiefly look for progress from the comparative investigation of corresponding processes in many different groups of animals. For the present we may well rest satisfied, if at any rate the meaning and significance of the two nuclear divisions are, *upon the whole*, recognized as true.

The future will teach us whether this is the case. In the meantime it promises well that, under the guidance of this thought, the apparently irreconcilable processes in *Ascaris* and *Pyrrhocoris* can be brought together under a common point of view. From this standpoint the two divisions of the germ-mother-cell signify *a period of reduction and of reconstruction of the idioplasm*. If reduction alone were needed—i. e. a diminution of the number of ids by half—a single division would have sufficed; but the second was rendered necessary in order to attain the greatest possible diversity in the germ-plasm. The accomplishment of these two ends is not always brought about by precisely the same course, but nature pursues somewhat

different routes, which however always meet at the principal stations, viz. the two nuclear divisions. We have learnt two of these routes, on the one hand from O. Hertwig, on the other from Henking: the observations of Flemming on the formation of spermatozoa in the salamander may possibly point to a third, those of Häcker to a fourth, but all agree in leading to the same end.

II. Inheritance in Parthenogenetic Reproduction.

The Processes of Maturation in Parthenogenetic Eggs and their Meaning.

It has for some years been recognized that the characteristic development of an egg into a fully formed individual is chiefly dependent on the nuclear substance, in so far as it is this which compels distinct differentiation in a cell-body which was previously, at any rate to some extent, indifferent, and which communicates to the total product of the egg-cell distinct modes of multiplication and development. When this became known it was obvious that the amount of nuclear substance possessed some significance, and that a certain mass of it was essential for the commencement of embryogeny in an egg-cell. I have therefore for some time agreed with Strasburger in seeking for the power of development without fertilization possessed by many ova, in the assumption that they contain an amount of germ-plasm which is twice as great as that present in eggs requiring fertilization, or that they can give rise to this amount by means of some process of growth. When the proof was afterwards afforded that parthenogenetic eggs produce only one polar body instead of two, I concluded, as is mentioned above, that the formation of the second polar body alone signified the halving of the number of ids which was required by the theory; for we could not assume that such a halving took place in parthenogenetic eggs. I looked upon the first halving of the nuclear substance, common to both kinds of eggs, as the removal of some nuclear substance which had no further use in either case, and the omission of the second nuclear division in parthenogenetic eggs I regarded as the means for retaining the amount of germ-plasm necessary for the egg to complete its course of embryogeny.

As I have already stated, that part of my former view of the significance of the polar divisions, which interprets the first as an extrusion of a specific ovogenetic nucleoplasm, must be abandoned. The facts of spermatogenesis, as we have recently learnt them from the researches of O. Hertwig, have overthrown these views, inasmuch as they prove that the nuclear idioplasm of all polar bodies, as well as that which is retained in the egg, must be germ-plasm. The polar divisions of the egg correspond exactly with the two divisions of the sperm-mother-cell, as will be seen at once by comparing Figs. I and II. By this means, four sperm-cells arise from the sperm-mother-cell, and of these four each contains half the number of idants characteristic of the species (see Fig. I, *F*). By means of the two polar divisions the egg-mother-cell similarly gives rise to the egg (Fig. II. *D E F*, 1), and the three polar cells (Fig. II. *D E F*, 2, 3, and 4), each of which contains the same number of idants, viz. two. As it cannot be doubted that the idioplasm of the four sperm-cells is germ-plasm, it must also follow that the same is true of the three polar bodies as well as of the ovum.

If then *one* polar body is always formed in regular parthenogenetic eggs, it might seem that an explanation is to be found by regarding it as a mere phyletic reminiscence. The question arises whether such a view is a just one, and in order to gain as clear a solution as is possible at the present time, I have added this chapter on parthenogenesis to the essay.

Spermatogenesis undoubtedly teaches us that the two 'reducing divisions' of the female germ-cell originally performed the primary duty of producing four distinct germ-cells from each mother-germ-cell. But spermatogenesis at the same time shows us that a very remarkable reduction of the idants accompanies these two divisions. The normal number of idants present in the mature spermatozoon is by this means reduced to half that in the primitive sperm-cell, and the result is reached by a most circuitous route, for the original number is first increased to double, and then, by two successive divisions, finally diminished to half.

When, however, we recognize that in normal parthenogenesis one of the two 'reducing divisions' is absent, while the other persists, we can hardly regard the latter as the meaningless reminiscence of a process which was full of significance in an

earlier phyletic stage: we cannot offer such an interpretation because this single polar division is found in *all* regular parthenogenetic eggs in which it has hitherto been sought for. It has been found, it is true, in eighteen species only, but these belong to different groups of the animal kingdom, viz. in eight Daphnids, a Branchiopod, two Ostracodes, three Rotifers, and four Insecta. In each of these a single polar body corresponding to those of the other seventeen, is expelled, and in each we must conclude that an apparently useless doubling of the idants takes place, together with an ensuing diminution to half, as is shown in the accompanying diagram (Fig. VIII), in which the normal number of idants has been fixed at four, in order to facilitate the comparison with Figs. I. and II. In view of the

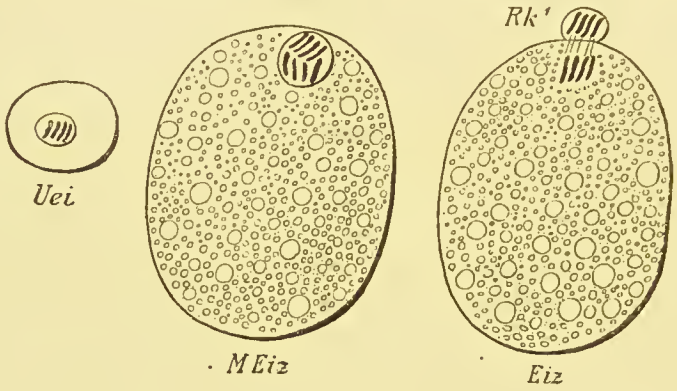


FIG. VIII.

Diagram of the maturation of the parthenogenetic egg.

regular occurrence of the phenomena in all the cases which have been examined, it is worth while enquiring whether a meaning and significance are not to be attributed to these most unexpected processes.

In the first chapter the attempt was made to show that the significance of the two 'reducing divisions,' in male and female germ-cells, is a double one, first, the *diminution* of the ids to half, and, secondly, the *arrangement* of the idants in fresh combinations. The first object might be gained by a single nuclear division, but the second would be attained only very incompletely, because a fresh combination of the idants occurs most readily, when associated with a previous doubling in number.

But this latter process renders *two* 'reducing divisions' necessary,—that is if the normal number of idants must be reduced to one half.

That there is no such reduction in regular parthenogenesis may be inferred from the large number of idants present in the parthenogenetic eggs of *Artemia salina*, viz. twenty-four or twenty-six. If a diminution to one half of the original number of idants normal for the species took place at each maturation, it is obvious that in each successive generation the idants would be reduced to half, and we should at the present day find only a single one left in *Artemia*. Either this polar division is not a 'reducing division,' or it is preceded by a doubling of the number of idants, just as in ova which require fertilization.

If this latter be true, it follows that in parthenogenesis we meet with a simple retention of the first of the two polar divisions which occur in other ova.

It is unfortunate that direct observation has not hitherto led to an entirely certain decision upon the point. Dr. Otto vom Rath has had the great kindness to examine, with this object in view, many of my old sections[1] of the parthenogenetic ova of *Artemia salina*, in order to find out those parts of them which were most important in this respect. From my earlier researches, conducted upon the same material, I was already aware that the germinal vesicle, after having approached the surface, contains a large number of chromatin granules, which are distributed with almost complete regularity. It was evident that these granules had not yet become the definite chromatosomes or idants, but that they were smaller and more numerous (Fig. IX. 1). In one germinal vesicle I counted 115 of them; in another, which was already changing into a spindle, I also found 115, all lying in the equatorial plane (Fig. IX. 2); in a third, 77; in a fourth, 70; and in a fifth, 57. Now in the equatorial plate of the polar spindle, from 48 to 52 spherical idants are always arranged in a double wreath (Fig. IX. 3 *a*). These must therefore have arisen from the fusion of several of the primary chromatin granules, and the great variation in the number of the latter must depend on the fact that the fusion was

[1] Weismann und Ischikawa, 'Weitere Untersuchungen zum Zahlengesetz der Richtungskörper;' Zoologische Jahrbücher, Bd. III. p. 575, 1888.

much further advanced in some of the germinal vesicles examined than it was in others. Half the number of 48 or 52 idants in the equatorial plate pass to one, and the other half to the other pole. If a diminution in the ids be characteristic of a 'reducing division,' it follows that this term can only be applied to the process which has just been described in *Artemia*, if the whole number of 48-52 idants have arisen directly from the primary chromatin granules: if, on the other hand, only 24-26 idants were so derived, and the equatorial plate was at first composed of a

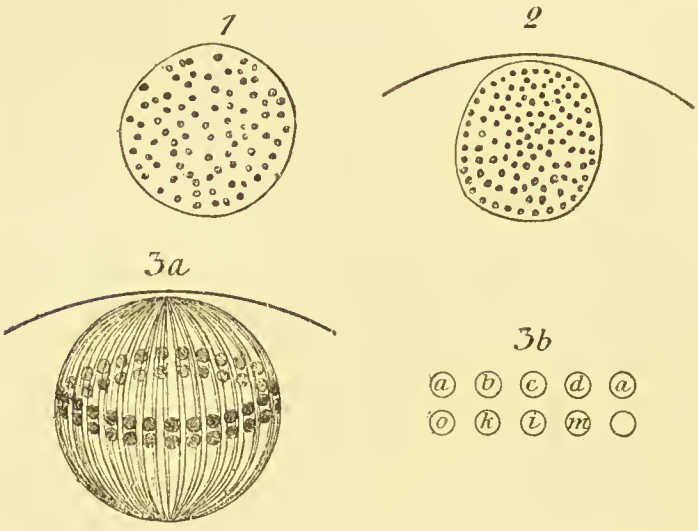


FIG. IX.

Artemia. Germinal vesicle of the parthenogenetic egg before and during polar division: partially diagrammatic, from my own preparations.

1. Numerous chromatin granules scattered through the whole thickness of the germinal vesicle. 2. Numerous chromatin granules (115) collected in the equatorial plane. 3 *a*. The same arranged in a double wreath of 52 idants in the polar spindle. 3 *b*. A part of the double wreath with the separate idants indicated by letters.

single wreath which was subsequently doubled by division of the idants, it would follow that the process would be an 'equal division.' In the latter case, the two idants lying over each other would be identical, i.e. composed of similar ids, and identical idants would pass into each daughter-nucleus. If, however, as in the former supposition, the two adjacent idants were independently derived, and therefore composed of different separate ids (chromatin granules), it is clear that the

idioplasmic construction of the two daughter-nuclei must be different.

Inasmuch as we cannot see whether the chromatin granules are made up of similar or different idioplasm, it follows that direct observation cannot conclusively settle whether we are dealing with an 'equal' or a 'reducing division.' Perhaps, however, we may succeed in decisively answering the question by other means, and investigations have already been undertaken with this special object; for the present we must rest content with conclusions based upon probability. Before everything we must make certain that the first division in eggs requiring fertilization is, in all cases, a 'reducing division.' At the present time *Artemia* reproduces sexually in many of its colonies, and hence in parthenogenetic colonies in which the eggs have lost the second polar division but have retained the first, it may be regarded as probable that the latter has kept its original form, i. e. that of a 'reducing division.'

Still further support for the above conclusions is found in the fact that Dr. vom Rath could never find *single* idants in the equatorial plate of the polar spindle of *Artemia*, but only *double* ones, each having the form of two large round bodies lying over each other (Fig. IX. 3 *a*).

If we now further consider that, at the commencement of the change of the germinal vesicle into the spindle, the chromatin granules lie scattered through the whole thickness of the former (Fig. IX. 1), and that they then fuse with one another, arranging themselves as a single layer in the equatorial plane of the spindle, in the form of an oval disc and not that of a simple wreath (Fig. IX. 2), and if we remember that they then pass into the arrangement of a double wreath (Fig. IX. 3 *a*), we are led to conclude that no two idants of this double wreath have arisen from the doubling by division of a single idant, as is the case in the usual 'equal division'; but that the idants of the oval equatorial plate, which arose independently of one another, have subsequently come to place themselves one upon the other in the form of a double wreath. If this conclusion be sound we have to do with a true 'reducing division.'

Hence we are justified in assuming as the most probable conclusion that a 'reducing division' takes place, and further-

more a division which is preceded by a doubling of the idants.

If this be so, we cannot doubt that the effect of the process must be similar to that which follows the corresponding processes in eggs which require fertilization, viz. the arrangement of idants in fresh combinations, as I attempted to show in the first chapter. We are thus led to the view that *in parthenogenetic as well as in sexual eggs a change may take place in the constitution of the germ-plasm during successive generations.*

If we start from that point in phyletic development at which parthenogenesis was first established, each idant in the original egg-cell was at that time composed of a series of different ids. Then, for the first time, these idants were not diminished to half the total number by two polar divisions, but, after being doubled in the egg-mother-cell and again reduced to half by the first polar division, their number in the mature ovum became the same as in the original egg-cell (see Fig. VIII). By this means a fresh combination was rendered possible and indeed unavoidable, unless we assume that the constituents of each pair of similar idants, which arose from the doubling of the previous idants, separated and united with those of the other pairs, forming two exactly similar groups which then respectively entered the two daughter-nuclei. This would be the result of an 'equal division' of the nucleus. Such a division is attained and ensured precisely because the doubling and division of the idants only takes place when they have already become arranged in the equatorial plate; but whenever the doubling has occurred beforehand, as is the case here, the two halves of an idant may indeed be occasionally shared between the two daughter nuclei, but they may also, just as readily, both pass into one and the same daughter-nucleus. From this freedom in the distribution of the idants follow the fresh combinations produced by the 'reducing division;' and the difference between an ordinary nuclear division, and the 'reducing division' which here takes place, depends essentially on the fact that, in the latter, *there is a shifting of the time at which the doubling of the idants occurs.*

Hence, if a species of *Artemia*, which had hitherto reproduced bisexually, were now to become parthenogenetic, then in spite

of the cessation, for all future time, of the mingling of the idants of the ovum with those of the spermatozoon, it would by no means follow that the offspring of a female would necessarily become 'identical twins.' With twenty different idants, if there are not the 377 million different combinations which calculation indicates, there would be nevertheless such a vast number of different combinations of idants, that two ova produced by the same mother could only rarely be identical. Among all the possible combinations, that very one might arise which existed in the original egg-cell of the mother herself and became expressed in her somatic cells. Such a combination would contain one idant of every kind, and such an ovum would give rise to an individual 'identical' with the mother, that is, to one similar to the mother in all respects except as regards those modifications of the inherited developmental tendencies, which are called forth by external circumstances.

We need not consider the unlikely suggestion, that all combinations are equally probable; if only it be conceded that any degree of difference is possible for the combinations of the germ-plasm, remarkable consequences follow. In the first place it appears that, in persistent pure parthenogenesis, the *number of different idants contained in the idioplasm must steadily diminish*, although perhaps at a very slow rate. If the number did not diminish new combinations could never arise, and that of the first parthenogenetic mother (*A*) would be retained indefinitely,—thus if there were twenty different idants (*a, b, c, d, e t*) the whole series would persist unchanged. If, however, another combination arose in the daughter (*B*), for example *a a b c d e t*, this would be brought about by one of the idants (*a* in this instance) becoming double, and then inasmuch as the total number of idants must remain the same, it follows that one of the others must be absent (for example *l*), or the number would be twenty-one instead of twenty. As a result of this the idant *l* would be wanting in all the descendants of *B*. If now we suppose that such a new combination, arising in this way by the omission of one idant and the reduplication of another, would not be formed in each generation, but only in every tenth, it follows that at the end of each series of ten generations, a fresh combination will arise by another omission and another reduplication, and so on, so that after a hundred

generations the number of *different* idants would have been diminished from twenty to ten, and the whole group would consist of ten pairs, for instance *aa*, *bb*, *cc*, *dd*, *ee*, *ff*, *gg*, *hh*, *ii*, *kk*, the idants in each pair being identical. In the course of later generations the number of different idants might be diminished still further, although more gradually.

We are thus led to believe that, in persistent parthenogenesis unbroken by bisexual reproduction, a great uniformity of germ-plasm will at length arise, and, as a result, a great uniformity of individuals. We cannot doubt this if we consider that each fresh simplification of the germ-plasm, when it has once appeared, is unable to revert towards complexity because fertilization, i. e. the introduction of foreign idants, is excluded. As soon as the 'reducing division' causes a single one out of the twenty maternal idants in the segmentation nucleus of the egg to become double, it has been shown above that one of the other idants must be irretrievably lost not only to the maternal germ-plasm and to the daughter, but also to the descendants of every generation. Among all the numerous possible combinations there is only one which leads to no diminution in the number of different idants, viz. the above-mentioned arrangement *a*, *b*, *c*, *d*, *e*, ... *t*, and this is an exact repetition of the maternal combination. Hence the diminution in the number of different idants is far more probable than the maintenance of the complete series, and this probability will be repeated in each successive generation, until only two kinds of idants remain in the germ-plasm. When, however, this point is reached [1], the reverse becomes true; for the probability that idants *a* alone, or *b* alone, would be left in the egg-nucleus by the 'reducing division' is much less than that both kinds would exist side by side.

This becomes clear if we consider a definite case. Instead of the twenty idants which have been assumed hitherto, let us take only half as many, viz. ten, and let us suppose that they have been already reduced to two different kinds, *a* and *b*. These double themselves in the mother-egg-cell to twenty—ten *a* and ten *b*. The following combinations are then possible for

[1] Even before this point is reached the probability begins to change.—A. W. 1892.

the germ-nucleus[1] of the egg produced by the 'reducing division,'—10 *a*; 9 *a* + 1 *b*; 8 *a* + 2 *b*; 7 *a* + 3 *b*; 6 *a* + 4 *b*; 5 *a* + 5 *b*; 4 *a* + 6 *b*; 3 *a* + 7 *b*; 2 *a* + 8 *b*; 1 *a* + 9 *b*; 10 *b*.

Hence we see that out of eleven possible combinations there are only two which contain one kind of idant alone: all others contain both. In the case of twenty idants there are only two out of forty-one combinations which contain either *a* or *b* alone; with forty idants, only two out of eighty-one.

Naturally this does not imply that the diminution to one kind of idant is improbable, but only that it would always remain largely in the minority, i. e. it would be found in relatively very few cases among the numerous eggs of the same mother. This must, however, change in the course of generations; for only in one out of the eleven combinations are *a* and *b* present in equal numbers, and only in the descendants of this single variety will the germ-plasm be chiefly made up of *a* and *b* in equal proportions: in all the other ten combinations, either *a* or *b* preponderates, and according to the extent of preponderance is the probability of a greater or less number of eggs which contain only *a* or only *b*. We may therefore maintain that, by continued parthenogenesis, the germ-plasm becomes ever simpler as regards its composition out of ids until it comes to consist of only two kinds of idants, but when once this composition has been reached it may be retained through long periods of time, during which there will be a changing majority, sometimes of one and sometimes of the other kind. Among the eggs of such a female there would always be some in which the germ-plasm would contain only one kind of idant.

Observations on Inheritance in Parthenogenesis.

When I developed the idea that the essential meaning of sexual reproduction was to ensure that amount of individual variability which is necessary for the phyletic development of the organic world by means of natural selection, I inferred that uninterrupted parthenogenetic reproduction would prevent the

[1] I have employed Strasburger's term 'germ-nucleus' instead of 'segmentation nucleus' which has been commonly used up to this time, as a general term for the nucleus of the mature egg from which embryonic development proceeds, whether parthenogenetic or amphigonic.

adaptation of a species to new conditions of life[1]. I argued that, the repeated mingling of two individualities being requisite to supply the process of selection with the necessary choice of combinations of individual qualities,—it follows that a choice of sufficient range will not be supplied when one and the same set of combinations are passed on by parthenogenesis, through long series of generations, to an ever increasing number of individuals. A number of 'identical' individuals would thus arise, that is individuals which contain a precisely similar fundamental stock of hereditary predispositions, and which, at most, can only be distinguished by transient peculiarities, viz. by those which are the consequence of external influences of various kinds upon the body during its progress towards maturity or after maturity has been reached. When writing on this subject, I expressed the opinion that 'all species with purely parthenogenetic reproduction are sure to die out; not, indeed, because of any failure in meeting the existing conditions of life, but because they are incapable of transforming themselves into new species, or, in fact, of adapting themselves to any new conditions[2].' I stated this conclusion in the strongest possible way although I thought that it might perhaps require subsequent modification, because, even at that time, I had already considered the possibility that the consequences of sexual reproduction of ancestors might affect their purely parthenogenetic descendants. But whether a simple rearrangement of the ids within the idants would suffice to call forth a fresh combination of individual peculiarities, appeared to me very doubtful; and yet this would have been the only alteration in the germ-plasm which we could have been led to suggest by the state of our knowledge at the time; for a 'reducing division' could not have been supposed to take place in parthenogenetic eggs, because we did not know that the number of the idants doubles before the occurrence of the first polar division, and because a halving of the number of idants, without any previous doubling, would necessarily, in a few generations, diminish their number to one. But now the case is different, and we may affirm that in parthenogenetic

[1] 'Die Bedeutung der sexuellen Fortpflanzung.' Jena, 1886, p. 58. Translated as the fifth essay. See Vol. I. p. 298.

[2] See Vol. I. p. 298.

generations, the combination of idants in the different germ-cells of one and the same mother can vary. We can therefore attribute even to parthenogenetic species a certain power of varying, although not to anything like the same extent as in bisexual species.

By the year 1884 I had commenced a series of experiments to decide the question of variability in purely parthenogenetic species. These experiments are still being carried on, and I hope that I may ultimately be able to make a more complete communication upon the subject. I chose for the purpose a species of *Cypris* (Ostracoda), which was characterized by striking and easily seen markings on the shell. I had at my disposal two very differently marked varieties of the species in question (*Cypris reptans*), which had been found in the natural state. The species appears to be purely parthenogenetic in this locality; at any rate I have never found a male, nor a female with spermatozoa in the *receptaculum seminis*[1]. The latter fact conclusively proves the complete absence of males; for in colonies of those species of *Cypris* which possess males, we always find the *receptacula seminis* of mature females filled with spermatozoa. Even if it were a mere coincidence that of the many hundreds of individuals examined, all proved to be females, the presence of spermatozoa in their *receptacula* would still have shown the presence of males, if any had existed in the locality. But the *receptacula* were, without exception, empty, at all times of the year, and under all the external conditions which obtained during my investigation of the colony.

My two sub-species are distinguished as follows (see Fig. X): variety *A* is lighter in colour, and there are only a few dark green spots of small size on the clay yellow ground-colour of the shell. Variety *B* appears dark green because the spots are so much larger that they expose only a little of the clay yellow ground-colour of the shell. In both varieties the spots agree precisely as to number and position; the difference between them is entirely quantitative, but it is considerable, so that the lighter *A* can be distinguished from the darker *B* with the naked eye at the first glance.

The experiment was conducted in the following way: I

[1] Compare my earlier paper 'Parthenogenese bei den Ostracoden;' Zool. Anzeiger, Bd. III. p. 81, 1880. See also Vol. I. p. 301, *note* 2.

placed a solitary individual in a small aquarium, and allowed it to multiply until the whole vessel was full of mature, egg-producing descendants. All the individuals of the colony were then passed in review, and the greater number were killed and preserved, one or more having been selected for breeding, and these were placed separately in fresh aquaria. In this way, in the course of seven years, many thousand individuals have passed through my hands; for the animals breed very rapidly and at all times of the year.

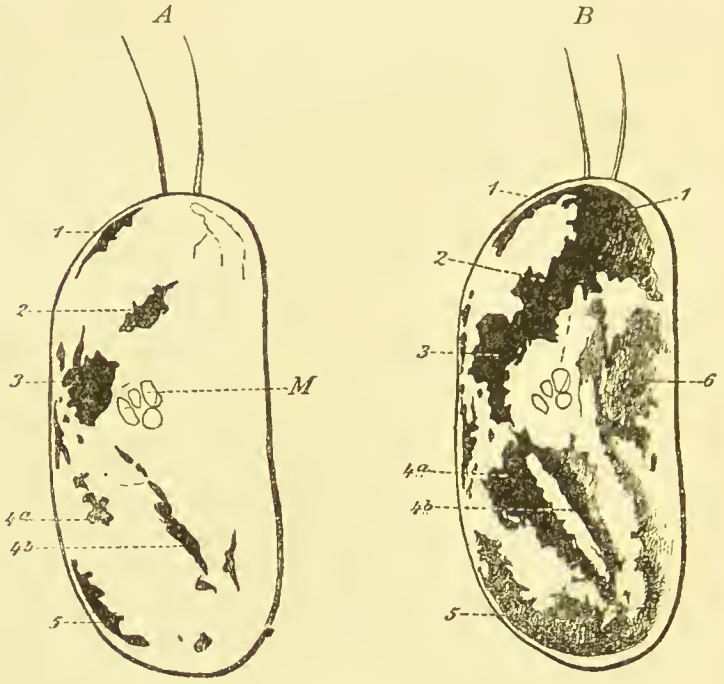


FIG. X.

Cypris reptans, Varieties *A* and *B*.

The first and most remarkable result is *the fact that the descendants of any one individual bear a very close resemblance to each other and to their ancestor.* I was not able to find any individuals which were precisely alike, although at first sight it often seemed that such was the case: minute differences, however, invariably existed as far as my observations reached, although they were often so small as to lead to the doubt whether they were due to different predispositions or to different nutriment, etc. And indeed no two individuals, not even 'identical' human

twins, can be exactly alike in this latter respect. Furthermore, as a rule, no changes made their appearance in course of the numerous generations during which the examination lasted, with an exception which will be immediately described. I now possess colonies of *A*, as well as of *B*, which cannot be distinguished from their ancestors in 1884, and which have therefore retained precisely the same markings as those of the original animals. If we reckon six generations to the year,—a number by no means excessive for breeding which took place in a room,—about forty generations will have been passed through since 1884.

I attempted at first to produce the two forms by artificial selection, breeding from the darkest individual of a colony of the variety *A*, and from the lightest of a colony of *B*, in the hope that, perhaps, in the course of generations, one variety might be changed into the other. But I obtained no decisive results, perhaps because I did not make my selection rightly; for the individuals are so very similar that it is often difficult and indeed hardly possible to decide upon those which possess the larger spots: perhaps also I mistook transient differences for inherited ones,—a confusion which, naturally enough, cannot be avoided.

I was therefore all the more astonished to find, in 1887, some individuals of the dark green variety *B* in the same aquarium with the light variety *A*, and therefore side by side with typical, light, clay-coloured individuals. At first I thought, although it was most improbable, that these had been accidentally introduced, but the greatest care had always been exercised in all these experiments. Furthermore, after the most painstaking precautions against such accidents, precautions which prevented all possibility of the eggs being misplaced, there presently appeared another similar case in a different aquarium containing the variety *A*, and, later on, yet another. In this last case it was possible to find in the aquarium intermediate forms between the two varieties, which had been wanting on the previous occasions. Again, in May of the present year, 1891, another case was observed in which a single animal, distinctly belonging to the dark sub-species, suddenly appeared among 540 mature *Cyprides* of the light variety. Five descendants of this individual closely resembled their mother.

For a long time I waited in vain for the converse result, viz. the appearance of light individuals of the variety *A* among those of the dark sub-species *B*, and I was coming to the opinion that the latter was the original form of both varieties, when, in the winter of 1890-91, a few typical individuals of *A* were found in a colony of the sub-species *B*, which had bred true for many years. This colony had arisen from a single dark individual which, in the course of seven years, had produced many hundreds of descendants all of the typical dark variety.

We might perhaps refer to the changing influence of external circumstances as an explanation of these divergences from the type, but any such interpretation is entirely excluded, because both forms made their appearance side by side in the same aquarium and under precisely the same external conditions. These remarkable phenomena must certainly be ascribed to internal causes, viz. to changes in the composition of the germ-plasm. The required explanation is by no means difficult when the subject is studied from the point of view afforded by the theory of idants: in fact these observations seem to me almost a proof of the validity of the opinion expressed above that a 'reducing division' occurs in parthenogenetic development, and that by its means a fresh combination of idants is brought about.

The fact that the variety *A* passes into *B* and conversely, *B* into *A*, leads to the conclusion that both types originated at a time when parthenogenesis was not the exclusive method of reproduction: had this been the case, the ids *a* could not have been included in the germ-plasm of animals of the type *B*, and conversely the ids *b* could not have existed in the type *A*. The explanation of the existence, side by side, of both kinds of ids, is only to be found in sexual reproduction which must have taken place at no very distant time.

Let us assume the simplest possible relationship, viz. that there are only four idants in the germ-plasm, of which three are wholly composed of ids of the type *A*, and one of ids of the type *B*. The four idants, *a a a b*, of the primitive germ-cell become doubled in the mother-germ-cell by longitudinal splitting, and give rise to the eight idants, *a a a a a a b b*. Let us further assume the most favourable case for reversion towards

the variety *B*, a reversion which would be possible in an egg in which the 'reducing division' takes place so that the combination of idants, *a a a a*, is removed in the polar body, while the combination, *a a b b*, remains in the germ-nucleus of the ovum. The primitive germ-cells of the next generation contain the same combination, *a a b b*, which is doubled in the mother-germ-cells to *a a a a b b b b*, and it is now clear that a 'reducing division' might occur, which would bring the four idants, *b b b b*, together into the germ-nucleus of an ovum, and from an egg containing germ-plasm with this constitution there must undoubtedly arise an individual of the variety *B*.

In this illustration, which is of course far too simple, reversion to the other variety might happen in the third generation. In those cases, however,—and they are the usual ones,—in which the number of idants is larger, and the proportion of variety *b* much smaller, the exclusive predominance of the latter can only take place far more slowly, and, as a rule, in much fewer cases; for it depends upon the chance of a combination of several idants *b* arising in certain ova, and of the survival to maturity of the individuals which develope from such eggs,—and these naturally must be far rarer than those with a largely predominating number of idants *a*. Furthermore, there is no certainty that, among the eggs produced by such individuals, any with an increased proportion of idants *b* would find a place.

These theoretical considerations harmonize well with the results of experiment. Variety *A* can give rise to descendants belonging to variety *B*, but this does not happen in all broods, and often only after the lapse of numerous generations. And the same is true of variety *B* in relation to the production of variety *A*. In both cases, relatively few individuals change into the other variety, and never all the descendants of one mother. In the aquarium in which such a transformation has occurred numerous individuals of the original form were invariably present,—a proof that it is always a rare exception for such extreme combinations of germ-plasm to be formed. When, however, this combination had once arisen, then such an individual gave rise, in all the cases observed, to offspring of *her own* type. Thus a mother which arose from variety *A*, but has passed over to variety *B*, behaves as though her ancestors had

belonged to the latter type. She produces offspring of the variety *B*, and the type is retained for many generations. In the illustration described above the type *B* would be retained indefinitely; for I assumed that only four idants were present, and that all these became of the variety *B*. In reality, however, this would occur but seldom, since the constitution of the germ-plasm must be far more complex: not only are the idants more numerous, but their composition out of ids does not remain entirely the same throughout long periods of time, as I have attempted to show in the first part of this essay.

If the idants are not entirely unchangeable in this respect, if, when they are freshly formed out of ids scattered through the nuclear network, there is an occasional alteration in the arrangement, we might then even assume that, by such displacements, a germ-plasm *a* which contains no purely *b* idants, but only a few ids belonging to the latter variety included within the *a* idants, could, nevertheless, in course of generations, undergo reversion to the variety *B*. But these are niceties, which it is as yet too early to consider; for we are only on the threshold of knowledge concerning hereditary phenomena in parthenogenesis.

But something at any rate has been proved; for we can safely affirm *that in parthenogenesis individual variation exists, which, as in bisexual reproduction, has its foundation in the composition of the germ-plasm itself, and thus depends on heredity, and is itself inheritable.* I thus erred in former times, in believing that purely parthenogenetic species entirely lacked the capability of transformation by means of selection; they do possess this power to a certain extent. I was, however, right upon the main point; for their capability of transformation must be much smaller than in bisexual species, as is evident from the observations described above as well as from theoretical considerations. The latter indicate that, in the course of generations, the constitution of the germ-plasm must ever become simpler; while the observations confirm this suggestion, inasmuch as they prove that a remarkable similarity exists between the descendants throughout numerous generations. The advantages of that complex intermingling of many individual predispositions which was brought about in the amphigonic ancestors of parthenogenetic species become gradually lost,

and we may maintain that *purely parthenogenetic species lose the capability of modifying themselves, more completely, the longer the pure parthenogenesis has continued.* So far as we can at present decide, this conclusion is in agreement with facts; inasmuch as no highly developed group of the zoological system, rich in species, is ever entirely composed of purely parthenogenetic species. In the animal kingdom, the Phyllopods and Ostracodes, among the Crustacea, are especially remarkable for the frequency of parthenogenetic reproduction. But *pure* parthenogenesis only occurs in isolated species, as in the above mentioned *Cypris reptans* and many other species of the same genus. Among the Phyllopods I only know of one species, *Limnadia Hermanni*, in which a male has never been found, and it is this very species which seems to have become extremely rare. In the other parthenogenetic species, in addition to the purely parthenogenetic colonies, there are always some which are composed of both sexes, as in *Apus cancriformis*; or else a regular alternation of parthenogenetic with bisexual generations takes place in the colony, as in almost all known species of Daphnids. The rich development of these groups of the zoological system has arisen under the uninterrupted influence of amphigonic reproduction, by means of which variations have been mingled together. It is just the same with the *Aphidae* (plant-lice and bark-lice), and with the *Cynipidae*. All these groups of animals contain a great variety of species, but, in all, a combination of individual characters takes place from time to time through the fertilization of ova, even though, as is often the case, many purely parthenogenetic generations intervene between the bisexual ones.

I believe that we find, in the tenacious retention of amphigonic reproduction by such species as the *Phylloxera*, a strong support of the validity of my theory as to the meaning of sexual reproduction. Those who still recognize in fertilization a renewal of vital strength, a rejuvenescence, do not require this conception of amphigony as an ever springing well of hereditary individual variation in order to understand its remarkable persistence. But those who agree with me in believing that the parthenogenesis of *Cypris reptans* which endures for forty consecutive generations is the refutation of any such idea of rejuvenescence, will hardly find another explanation of this tenacious persist-

ence. Thus, let us call to mind *Phylloxera* and its allies, in which many purely parthenogenetic generations follow one another every year and bring about an immense increase of individuals, to be finally succeeded by a single sexual generation of insignificant wingless males and females without mouth appendages, which have nothing to do but pair immediately after birth in order to produce the fertilized ova. Thus, sexual reproduction is retained in spite of the fact that no increase, but rather a decrease, in the number of individuals is, in these cases, brought about by its means, just as in the conjugation of the lower unicellular organisms. Some great advantage must therefore follow from its retention.

It may, however, be lost, and we cannot at present decide whether the immediate advantages which pure parthenogenesis affords are sufficiently important to justify the disappearance of those arrangements by which the power of increasing variation is guaranteed. We cannot penetrate far enough into the details of the struggle for existence to be able to determine whether a species can in any way fall into so critical a position that its survival can only be brought about by that excessively rapid rate of multiplication which is rendered possible by pure parthenogenesis. In such a case amphigony would have to be abandoned, for the only choice would be that between extinction and parthenogenesis, and the future of the species would be to some extent sacrificed to its temporary maintenance. But I do not by any means wish to imply that this is the only way in which the omission of sexual reproduction can be understood. The question is only opened, and we cannot yet claim to have answered it satisfactorily.

We must now turn our attention for a short time to the vegetable world. Unfortunately, there are not, as far as I am aware, any available observations on plants which give us reliable information as to those processes of maturation of male and female sexual cells which have now been described in the animal kingdom. Certainly Strasburger and others years ago described cell-divisions of mother-cells, both male and female, which resemble the 'reducing divisions' of mother-cells in animals; but whether, in this case also, a doubling of the idants precedes their twice-repeated division into halves, appears to be unknown. If we may assume that such a result is by some

means ensured, that the number of ids is halved, and that their fresh grouping is thereby provided for, we cannot at any rate predict whether the process is conducted in precisely the same way as in animals. We ought perhaps rather to expect that some deviation from the reducing methods customary among animals would here be met with, a deviation which would render the meaning and significance of the latter even clearer and more definite.

We are justified, however, in believing that, in the cases of plant parthenogenesis, the amount of variation will diminish, together with the capability of adaptation by the operation of natural selection. Adaptations caused by direct influence on the germ-plasm are naturally conceivable in these as in other cases, but at present we know so little about such changes, whether produced by climatic or nutritive conditions, that it is impossible to determine how much may be implied by them.

Ten years ago parthenogenesis was doubted by botanists, or at any rate was regarded as very rare, and only to be found in cultivated plants, such as *Pteris eretica*, in which a certain tendency to degenerate was recognizable, or, at any rate, in which the structural and functional arrangements were no longer subject to the operation of natural selection. But we now recognize that a whole group of fungi, the Saprolegniae, 'including several genera and many species, are parthenogenetic.' Among the Ascomycetes 'it is admitted that many genera and species . . . are certainly asexual.' Amphigonic reproduction in the Æcidiomycetes is 'extremely doubtful,' while the Basidiomycetes 'afford an example of a vast family of plants, of the most varied form and habit, including hundreds of genera and species, in which, so far as minute and long-continued investigation has shown, there is not, and probably never has been, any trace of a sexual process[1].'

If the last statement be correct, it is impossible to maintain the existence of parthenogenesis in the Basidiomycetes; for this method implies the sexual reproduction of ancestors as its origin. Parthenogenesis is virgin reproduction, and signifies a power of development without fertilization possessed by female germ-cells. Parthenogenesis has arisen from bisexual reproduction by the elimination of the male and

[1] See Vines in 'Nature,' 1889 (Oct. 24), p. 626.

the male germ-cells; with the knowledge we now possess there can be no doubt upon this question. Not every unicellular germ is phyletically an ovum. We ought to recognize and apply to the botanical world the difference between parthenogenesis and asexual reproduction from unicellular germs. This distinction has not been made with any completeness, as we see in the passages quoted above from Professor Vines, and hence it is impossible to draw any safe conclusions from the asexual reproduction of the above-named fungi and from the fact of the phyletic development of numerous genera and species,—as to the amount of variation provided by heredity in parthenogenetic reproduction. The conditions of life among fungi are well known to differ markedly from those of most other plants, and it is not inconceivable that these may be associated with the disappearance or absence of amphigony; for the peculiar conditions of life may exercise an unusually strong direct influence upon the germ-plasm, and may thus render it variable. We know that variability is induced in other plants when they are submitted to very favourable nutritive conditions. But the researches of botanists must not be anticipated by these conjectures.

The Origin of Parthenogenetic Eggs from those which require Fertilization.

As I have already stated, parthenogenesis must have arisen from sexual reproduction. Those cells which develope parthenogenetically are female germ-cells which have gained the power of producing new organisms without fertilization. We must now enquire how this change has been brought about.

I must first allude to the gonoplastid theory, of which the principle has been proved to be untenable, but which is nevertheless correct in certain aspects, at least in the form in which Balfour conceived it. This thoughtful writer expressed the idea that the arrangement of polar bodies might have been brought about by nature, *in order to prevent parthenogenesis*. He therefore imagined that parthenogenetic development would ensue if the polar bodies, containing the supposed 'male principle,' remained in the egg. If, however, the facts are somewhat different, in so far as the polar divisions of the egg have been

from the first an adaptation to fertilization, they have at any rate the effect of checking the power of development in the egg, so that, in a certain sense, we may maintain that their expulsion prevents parthenogenesis. On the other hand, we are now aware that a polar body is expelled from the parthenogenetic egg, while the difference between this and the egg requiring fertilization lies in the fact that a second polar body is expelled from the latter; but the correct idea nevertheless remains that something indispensable for the power of development is removed from the egg. According to our present views this is not the unknown 'male principle,' but a certain quantity of germ-plasm.

When we begin to enquire into the manner in which the power of parthenogenetic development was gained by an egg which required fertilization from the most remote time at which multicellular beings existed, the first thought that strikes us is, —*might not this have been brought about by the suppression of the second polar division?* If this happened, the first polar division would cause a diminution to the normal number of the previously doubled idants, and the second polar division being absent, the egg-cell would retain precisely as much nuclear material as it would have contained if fertilization had followed the expulsion of the second polar body. Since, then, regular parthenogenetic eggs invariably possess only one polar body, this supposition attains a high degree of probability. There are, however, facts which show that parthenogenesis may be acquired in another way.

Blochmann has observed, as is well known, that when the egg of the queen-bee is deposited in the cell of a drone, the same course of maturation is pursued as when it is laid in a female cell. In both cases two polar nuclei are formed, in both the nuclear substance is halved twice successively. In the case of the unfertilized male egg, the nucleus which remains after the second division possesses the power of becoming the germ-nucleus, and of developing; while the female egg is only able to enter upon embryogeny after the fusion of its nucleus with that of the fertilizing spermatozoon.

The eggs of Lepidoptera behave in a somewhat similar way; in the great majority of cases they require fertilization, but some can develope parthenogenetically. In the case of *Liparis dispar*,

Platner found that such parthenogenetic eggs, like those which require fertilization, expel two primary polar bodies.

From this it is clear that parthenogenesis is possible, even when the quantity of germ-plasm in the egg has been reduced to half. Rolph, in his day, attributed parthenogenesis to better nourishment; Strasburger surmised, in adapting these thoughts to the significance of nuclear substance, which had in the meantime been recognized, that 'favourable conditions of nutrition counterbalanced the deficiency of nuclear idioplasm.' He assumed that the nucleoplasm was reduced to half, even in parthenogenetic eggs, and that 'the egg-nucleus after its reduction to half was unable to initiate the processes of development in the cell-body.' It was in these very cases of exceptional parthenogenesis in single ova that I expressed the definite opinion that the difference between eggs which are capable of parthenogenetic development and those which are not, must be quantitative and not qualitative[1]. I concluded from the facts connected with exceptional parthenogenesis, that a *certain amount of germ-plasm* must be contained in the egg-nucleus if it is to be in the position of entering upon embryogeny, and of completing it, and that, in these exceptional cases of parthenogenetic development, the germ-plasm in the egg, after having been reduced to half its normal amount, possesses, in some unusual way, the power of increasing to double. I am well aware that many facts subsequently discovered appear to be opposed to this suggestion, but I believe they only appear to be so. For example, my views as to the two varieties of *Ascaris megalocephala* might be cited in opposition; of these varieties one possesses two idants in the segmentation nucleus, the other four. We might conclude from this that the *amount* of nuclear matter does not control entrance upon development, but some other cause,—perhaps those 'spheres of attraction' and the central-bodies which E. van Beneden discovered lying in them, and which Boveri has called the centrosomata. I do not dispute the significance of these remarkable bodies in relation to the commencement of nuclear division, but do we know whence they come, and whether they are not perhaps, on their part, controlled by the nuclear idioplasm (germ-plasm)?

[1] 'Continuity of Germ-plasm.' Jena, 1885, p. 90. Translated as the fourth essay; see Vol. I. p. 231.

I hold that this is not only possible, but even probable. The difference between the embryogenies of two allied species not only depends upon the characteristic differentiation of the single cells which compose the body, but also equally upon their number, both relatively and absolutely, in all parts of the body. One and the same part of the body may be long in one species, and short in another; more cells will be required for the construction of the former than for the latter, or, in other words, the earliest embryonic cells of this part of the body must multiply more rapidly in one species than the other. If now this mode of cell-division is determined by the specific nature of the above-named centrosomata of such cells, it follows that embyrogeny must be essentially controlled by the centrosoma, i.e. by a part which lies in the cell-body, and which we have hitherto regarded as a part of it.

We do not however know that this is really the case; possibly the centrosoma may have been originally derived from the nucleus. But even if we admit that it is, not only in position but also in origin, a part of the cell-body, we must nevertheless believe that its activity is dependent on the nucleus and nuclear substance. The centrosomata form the active, and thus the chief part of that remarkable mechanism which controls nuclear division. If this mechanism is once set in motion, it completes the division in the manner described above, just as a spinning machine twists its numerous threads, but that the apparatus is put in motion, does not depend upon itself, but obviously upon the internal conditions of the cell, which react upon the mechanism for division, so that it is compelled to enter upon activity. How can we otherwise understand Flemming's recent discovery that the centrosoma is always present in the cell-body, but only periodically initiates the nuclear division? Now the internal condition of the cell is, as we are aware, primarily determined, in all its qualities, by the nuclear substance, and consequently the centrosoma and the dependent mechanism for division are ultimately controlled by the nuclear substance, which regulates the rhythm of cell-division and dominates the whole structure of the organism. If it were otherwise, this nuclear material could not be the hereditary substance—the material basis of hereditary qualities [1].

[1] Fol's recent observation that the centrosomata of ovum and spermato-

We know little at present about the detail of processes going on in the cell, and mediating between nucleus and cell-body and between this latter and the centrosoma; but I believe that this at any rate may be regarded as certain, viz. that everything which occurs in the cell, including the rhythm and the manner of its multiplication, depends upon the nuclear substance. But if this be so we cannot neglect its quantity: *there must be a minimum amount of nuclear substance below which the control over the vital processes of the cell cannot be completely exercised.* If this be correct, we shall be justified in explaining the cases of exceptional parthenogenesis by the assumption, that the nucleoplasm of certain eggs possesses a greater power of growth than that of the majority of eggs of the same species; while in the case of the bee, every ovum possesses a power of growth sufficient to double its nuclear substance, after reduction to half,—that is, when it is not raised to the full amount by means of fertilization.

This explanation, so far as I can see, is in complete agreement with all the facts of the case, and especially with the observations by which various investigators were, in earlier times, enabled to show that the unfertilized eggs of various species of animals, e. g. the silk-worm moth (*Bombyx mori*), frequently enter upon an embryonic development which is never completed, but is arrested at an earlier or later stage. This becomes intelligible if we suppose that the cell is controlled by the *quantity* of nucleoplasm. According as the germ-plasm, diminished to half by expulsion of the two polar bodies, possesses a weaker or stronger power of growth, it will follow that its quantity will be sufficient to bring about the first divisions of the ovum, but not to complete the whole em-

zoon divide during fertilization, and that the halves fuse together to form the two pole-bodies of the first segmentation spindle, agrees well with this view. Fol, 'La Quadrille des Centres,' Genève, 1891. Moreover this observation does not include anything which need surprise us, because nothing takes place except that which precedes every nuclear division, viz. the doubling of the centrosoma. The two sexual nuclei behave exactly like any other nuclei: even as regards outward appearance they may retain their independence for a long time in certain species, and fusion into a single nucleus only occurs at a later stage of segmentation. The evidence for this statement is afforded by observations upon *Cyclopidae* by Dr. Ischikawa, communicated to me in letters, and independently by the researches of my assistant, Dr. Häcker, upon the same animals.

bryogeny, or, on the other hand, will suffice to bring it to completion. In an earlier work I have endeavoured to render this theoretically intelligible and must here refer to that attempt[1]. But I should wish to add in this place that I have, since then, convinced myself that the view which I urged is correct. In conjunction with Dr. Ischikawa, I have examined the eggs of many Lepidoptera as to the power of development without fertilization: we observed that, as a matter of fact, some eggs entered upon embryogeny, which was, however, sooner or later arrested in most of them, only a very few reaching the caterpillar stage. Out of about a hundred unfertilized ova of *Aglia tau*, we obtained only a single fully developed caterpillar, many eggs shrivelled after a few days, while others remained plump: in most of the latter the yolk contained a large number of blastoderm cells; for a whole month these eggs developed very slowly and irregularly[2], but they finally shrivelled and decayed. The ova of one and the same female vary in respect to their powers of parthenogenetic development, and such individual differences cannot lie in the yolk, inasmuch as this nutritive material is distributed in the same manner and in equal amount in all eggs: they must rather be referred to differences in the rate of growth of the germ-plasm; at any rate, I cannot imagine any other cause which might account for them.

But this conclusion does not carry the implication that parthenogenesis could not have arisen by the method which was first indicated, viz. by the suppression of the second polar body. Indeed, I am inclined to believe that regular parthenogenesis has invariably arisen in this way; for otherwise the absence of the second polar body would not be so common, nor would it be without exception. This method cannot however obtain in facultative parthenogenesis, because that very egg which is capable of parthenogenetic development must also remain capable of fertilization. But this latter capability involves that reduction of the germ-plasm which occurs by means of the second polar division. In those cases in which parthenogenesis became necessary, and at the same time the capacity for fertili-

[1] Continuity of Germ-plasm.' Jena, 1885, pp. 92 et seqq. Translated as the fourth essay; see Vol. I. pp. 231 et seqq.

[2] The observations were not directed to the details of embryogeny.

zation had to be retained, there remained nothing except to strengthen the ordinary process of egg-maturation and thus to endow the retained half of the germ-plasm with increased powers of growth.

III. Amphimixis as the Significance of Conjugation and Fertilization.

The Facts of Conjugation.

Biologists have been, for some time, in the habit of comparing the conjugation of unicellular organisms with the sexual reproduction of multicellular forms of life, and of regarding them as to some extent equivalent. There was an obvious comparison between the more or less complete fusion of two of the former, and the coalescence of the two sexual cells of the latter; and this conception was strengthened when observation appeared to prove that the reproduction of unicellular beings by means of fission could not continue indefinitely, unless conjugation took place from time to time. Conjugation was looked upon as a 'fertilizing' process which endowed the organism anew with the capacity for fission, not once only but repeatedly, just as fertilization in multicellular beings renders possible the production of numerous cell-generations, constituting embryogeny. The cell material which, in the latter case, is made use of in building up the multicellular organism, appears in the former as a succession of many generations of unicellular beings; but, in both cases, the capacity for such cell multiplication depends upon the previous occurrence of a fusion of cells, thus originating the life-giving force which renders reproduction possible.

The above sentences form an approximate statement of the views which, with some individual differences, have obtained among biologists during the decade before the last. Even the remarkable discoveries of Bütschli on the conjugation of Infusoria led to no essential modification, although they taught us to recognize the mysterious nuclear changes, the analogy of which to the processes of fertilization was then unknown.

However, mainly in consequence of the observations of the brothers Hertwig, of Fol and of E. van Beneden, this analogy is now recognized, and we may admit that the connection between

conjugation and fertilization is firmly established, more especially since the investigations on the conjugation of Infusoria, begun by Bütschli, have been carried to a high degree of completeness by the work of Balbiani, Engelmann, Gruber, R. Hertwig, and above all by the exhaustive and wonderful investigations of Maupas[1].

But even if we may at length regard the agreement between the processes of reproduction and conjugation as firmly established, and the ideas of an earlier date confirmed, we cannot, in my opinion, retain the former conceptions as to the deeper significance of these two processes. Both conjugation and fertilization appear in an entirely new light if,—leaving behind all ancient prejudices, and without bias—we examine and compare them from the standpoint of our present knowledge. Each process throws light upon the other, and the true meaning of both is thus made clear.

I will first briefly recapitulate the facts of conjugation as established by Maupas and ably confirmed and extended by R. Hertwig, and I have therefore appended in Fig. XI. a free rendering of Maupas' figures, which illustrate the changes in the nucleus accompanying the conjugation of *Paramaecium caudatum*. *M* indicates the macronucleus, *m* the micronucleus; m^1 and m^2, in figure 3, signify the two daughter-nuclei which arise from the first division of the micronucleus; m^1—m^4, in figure 4, the four grand-daughter-nuclei of the same, derived from the fission of the daughter-nuclei. In figure 5, three of these, m^1—m^3, are already disintegrating, while the fourth, m^4, is drawn out into a spindle preparatory to division, and the consequent formation of the two reproductive nuclei, Cop^1 and Cop^2. Figure 6 shows the reciprocal transference of the male reproductive nucleus from each animal into the other; and

[1] We should read the admirable work of Maupas with even greater satisfaction if it contained fewer reflexions upon those who have worked in the same field. Maupas should not have forgotten that even the ablest cannot avoid error, and that it is the fate of all work, even the most excellent, to be in time surpassed;—for upon this the whole advance of science depends. We may correct the mistakes of our predecessors without forgetting that we stand on their shoulders. The very power we possess of improving on them is largely due to the fact that they have placed their successors upon a higher level than that from which they started themselves, and it is but a poor return for this to label their work 'superficial,' 'inaccurate,' &c., &c.

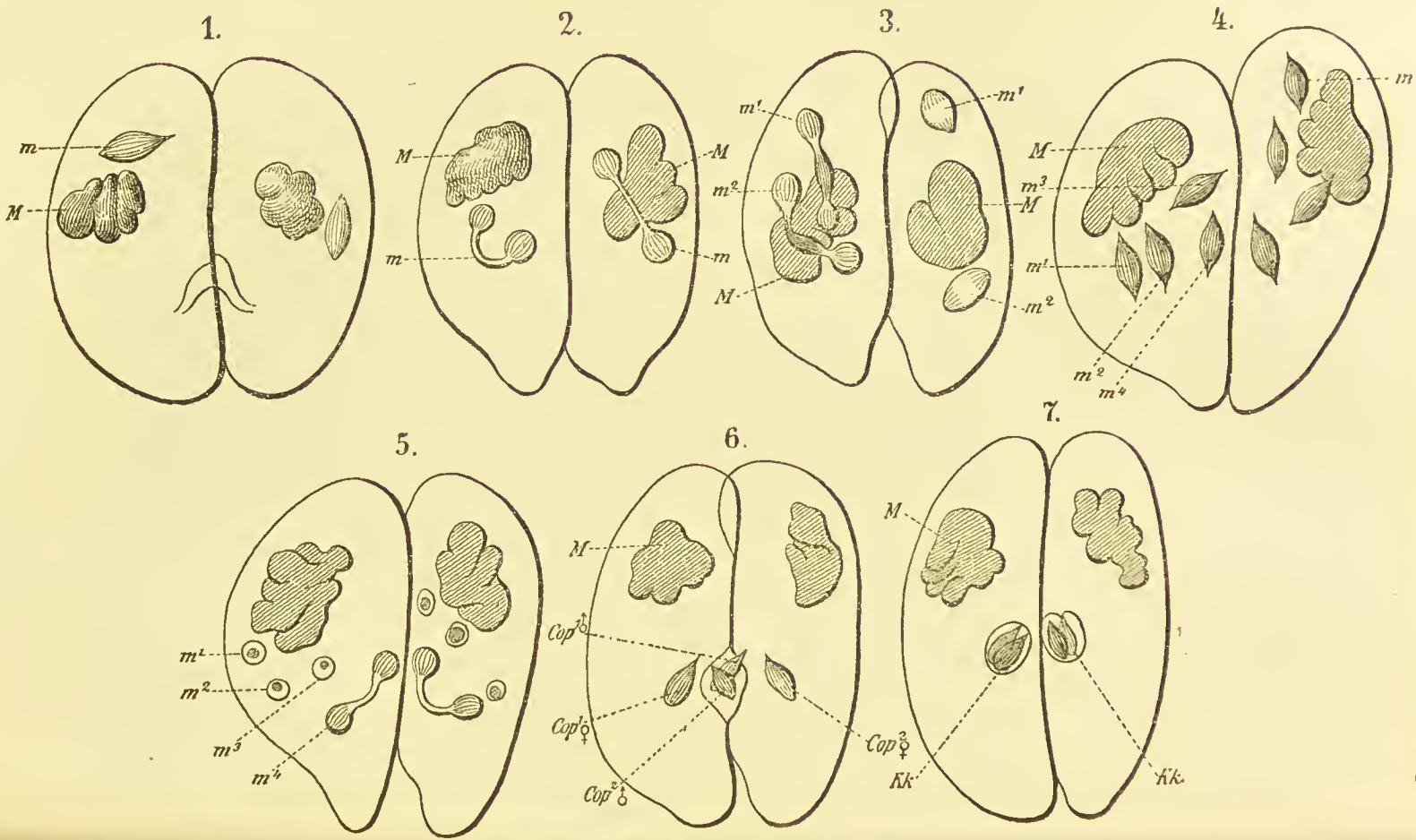


FIG. XI.—The conjugation of *Paramaecium caudatum* (modified from Maupas). *M*—Macronucleus *m*—micronucleus

figure 7, the fusion of the male and female nuclei to form the germ-nucleus, *Kk*.

The essential part of this process is shown even more clearly in the annexed diagrammatic representation of the changes undergone by the micronucleus, which Maupas has constructed for *Colpidium truncatum*. Fig. XII. illustrates diagrammatically the nuclear changes of two conjugating individuals of this species. The black spheres represent the persistent nuclei, while the circles stand for those which disintegrate and disappear. Similar processes take place in each individual of the conjugating pair. The micronucleus first grows from its previous small size, A^1, to a considerable bulk, and it is shown in A^2 as ready for the first fission, producing the two nuclei (*B*). Each of these daughter-nuclei again divides, and thus the four grand-daughter-nuclei arise (*C*). Three of these disintegrate and disappear, while one divides and produces two nuclei (*D*) comparable with the sperm- and egg-nuclei of Metazoa. We may call these the male and female reproductive nuclei, and may regard that as the male which leaves the animal in which it had its birth and enters the other organism in order to fuse with its female reproductive nucleus. This fusion, represented at *E* in the diagram, leads to the production of the 'combination nucleus[1],' the analogue of the 'germ-nucleus' of fertilization.

The old macronucleus disintegrates and is absorbed, but by the double division of the 'combination-nucleus' two new macro- and two new micronuclei arise, preliminary to the first fission of the whole animal which now commences.

The essential part of the whole process is the fusion of two equal amounts of nuclear substance, the one derived from one animal and the other from another, and the formation from this nuclear substance, thus derived from two individuals, of the nuclei which dominate the animals after conjugation. This harmonizes with the process of fertilization in that here also two equal masses of nuclear substance, derived from two different individuals, unite to form the new germ-nucleus. Now that we at length recognize that the 'nuclear substance' is the ruling principle of the cell, that Nägeli's 'idioplasm' is the

[1] By this term I mean a nucleus which has arisen by amphimixis, and consists of equal amounts of idioplasm from two individuals.

hereditary substance, we are enabled to state that the essence of both conjugation and fertilization is nothing more than a *mingling of the hereditary substances of two individuals.* I pro-

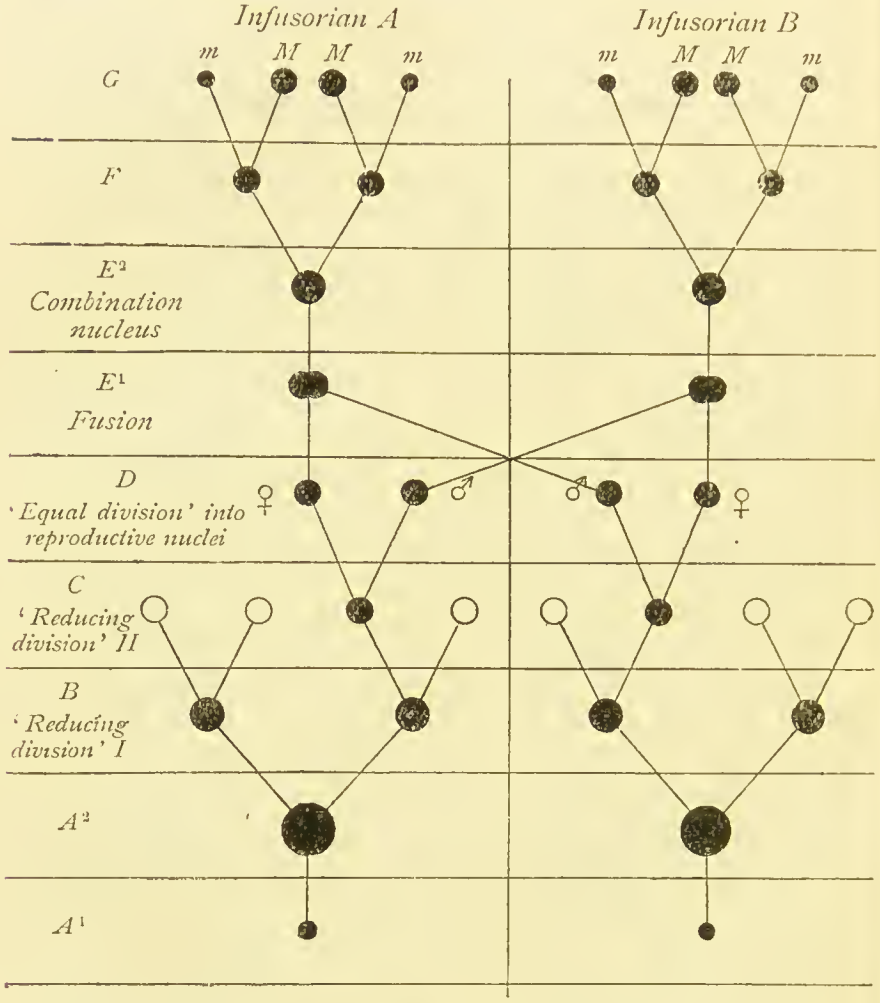


FIG. XII.

Diagram of the changes undergone by the micronucleus during the conjugation of a Ciliate Infusorian; (after the diagram given by Maupas in the case of *Colpidium truncatum*).

pose to introduce the term *Amphimixis* to indicate such a process of mingling of the idioplasm from two individuals. The usefulness and indeed the necessity for some such special

term will soon be apparent. If we next consider the phenomena which have been directly observed, we find that, in spite of the already mentioned fundamental agreement between the two forms of amphimixis (conjugation and fertilization), there are some not unimportant differences between them.

This is partly due to the fact that those Infusoria which have supplied the most familiar examples of conjugation, possess two kinds of nuclei, the macronucleus and the micronucleus. To the former is attributed the vegetative functions, while the latter has been termed the 'generative nucleus.' It is certain that both nuclei proceed from the same material, viz. from the combination-nucleus of the animals after conjugation, that is, from a germ-nucleus. It is thus established that their differentiation depends on the principle of division of labour, and Maupas probably comes near the truth when he attributes to the macronucleus a ' bon fonctionnement des organes de la vie végétative et à la forme individuelle,'—a conception which does not precisely coincide with that of Bütschli, Gruber, and Hertwig, who regard it as an 'assimilative nucleus' only. Ascertained facts indicate that the micronucleus, in the first place, sub-serves amphimixis; for it and it alone produces the reproductive nuclei. But we must beware of restricting its activity to this single function. Numerous facts tend to show that it has another function, in addition to that which relates to the periods of conjugation. In many species there is not one micronucleus, but two of them, which are found regularly through the whole period of fission, although only one takes part in conjugation, while the other disintegrates. In other species numerous micronuclei exist, and in *Stentor Roeselii* there are eight-and-twenty regularly distributed through the whole animal. This indicates that during the period of multiplication of the Infusorian its mass of idioplasm must be greater than during the period of conjugation, and this again points to some special activity during the former period. I do not know of what kind this activity is, and do not care to speculate, since the question has no bearing upon our present subject. This much, however, is determined, that as regards conjugation, the micronuclei bring about *the continuity of the germ-plasm*. Among the Metazoa this continuity is not, in many cases, effected so directly and visibly, but it is brought about, as I believe, by

minute invisible masses of germ-plasm, which arise from the egg and are afterwards carried on, mingled with the contents of certain somatic cells. In these cases the origin of such masses in the egg can only be conjectured, but in conjugation observation shows that a part of the idioplasm is, as a matter of fact, set apart in the form of micronuclei for the use of the next generation. The nuclear substance of the micronucleus alone is undying, and continues the vital processes without limit, while the macronucleus behaves, in this respect, in an entirely different manner.

In the Metazoa the whole cellular structure of the body—the soma—is worn out by the processes of life, and suffers natural death: in just the same way the Infusorian macronucleus cannot continue its functions for unlimited generations, but must be renewed from time to time; and indeed, as we have already seen, it is formed anew from the combination nucleus which originates in the amphimixis of the two reproductive nuclei. During the formation of the new macronucleus the old one is destroyed and disappears. These are processes which have no analogy with fertilization: I shall return to their deeper significance later on.

A further difference between fertilization and conjugation lies in the fact that the reproductive nuclei of Infusoria arise from the thrice-repeated nuclear division of the micronucleus, while the nuclei of the egg- and sperm-cells of Metazoa are derived from the twice-repeated division of the mother-cell.

Meaning of the Phenomena.

It may appear decidedly premature to attempt an explanation of the above-mentioned differences and resemblances between the two forms of amphimixis; but I am willing to undertake this responsibility, if only to give a fixed direction to further investigation. If I abandon all the theoretical conceptions of fertilization and heredity developed in my earlier writings, I do not believe that we need, on this account, give up all views upon the processes of conjugation as they are known to-day, but rather that future research will be more profitable if we endeavour to test some settled theory, instead of making observations with no object in view.

The preparatory divisions of the micronucleus have been

frequently compared to the formation of polar bodies in the animal egg. If we consider the physiological significance of the two processes, this comparison is certainly striking, but it is incorrect to push it so far as the attempt to homologize the separate phases [1] and to explain them as morphologically equivalent; for all homology between two living forms depends upon their similar origin, and no one can believe that the higher animals have originated from the Ciliate Infusoria. The kind of conjugation exhibited by the latter is widely removed from its simplest form, occurring among the lower Protozoa, and any direct connection between the conjugation of Ciliata and the sexual reproduction of Metazoa cannot be assumed. Hence any attempt to homologize the *separate phases* of these two kinds of amphimixis must fail, although the processes are *in their essence* certainly homologous; for both have sprung from the same root,—the conjugation of the lowest forms of living beings.

I shall, however, attempt to show that many of the details of the two processes possess *a corresponding significance*, which must therefore be very deeply rooted, inasmuch as similar events have not been called forth by a common origin but by physiological necessity; just as the eyes discovered by Semper [2] on the back of certain slug-like Molluscs (*Oncidium*) resemble Vertebrate eyes, not because the Molluscs have been derived from Vertebrates, or *vice versa*, but because the necessity for eyes has called forth such a structure out of the foundation provided by the fundamental nature of light and the histological details of the *Oncidium's* dorsal surface.

I find the foundation of my explanation of the nuclear divisions accompanying amphimixis in the fact that *the micronucleus of Infusoria possesses nuclear rods or idants*, the proof of which we owe to the researches of Pfitzner [3], R. Bergh [4], Maupas, and Balbiani [5]. This fact indicates that the structure of the idio-

[1] A. Giard, 'Sur les globules polaires et les Homologues de ces éléments chez les infusoires ciliés.' Paris, 1890.

[2] C. Semper, 'Ueber Schneckenaugen vom Wirbelthiertypus.'

[3] Pfitzner, 'Zur Kenntniss der Kerntheilung von *Opalina ranarum*.' Morph. Jahrbuch, Bd. XI. p. 454; 1886.

[4] R. Bergh, 'Recherches sur les noyaux de l'Urostyla.' Liège, 1889.

[5] Balbiani, 'Sur la structure intime du noyau de *Loxophyllum meleagris*.' Zool. Anzeiger, No. 329 and 330; 1890.

plasm in Infusoria corresponds with that in Metazoa, and we are justified in transferring to these Protozoa the conceptions at which we have arrived as to the relation and significance of the Metazoan idioplasm, and, above all, the conception of *the individual difference of nuclear idants.*

R. Bergh's researches upon *Urostyla grandis* prove that the spindle of the micronucleus contains, during division, nine rod-like idants (see his fig. 9). Since, however, only one side of the spindle is represented in the drawing, the total number of idants must be eighteen. All who have observed the phenomena of conjugation agree that the first preparatory change in the micronucleus consists in a *considerable enlargement*[1]. Maupas[2] gives a series of fourteen figures illustrating this increase in the size of the micronucleus and its conversion into a spindle, and he calculates that, during this period, its original mass is multiplied eight-fold.

Richard Hertwig[3], who has directed special attention to this point, found that the micronucleus of a *Paramaecium*, immediately after division, was extremely small,—less than three microns[4] in diameter, while that of the micronucleus of an animal previous to conjugation was about seventy-five microns.

This enormous increase in size largely depends on the growth of the achromatin substance which plays a most essential and remarkable part in the subsequent divisions, but it does not therefore follow that there is no simultaneous increase in the idioplasm. I assume that the increase of the micronucleus is connected with *a doubling of the idants by longitudinal division.* There is at present no proof of this assumption; for no one has

[1] Schewiakoff's beautiful observations ('Ueber die karyokinetische Kerntheilung der *Euglypha alveolata*;' Morpholog. Jahrbuch, Bd. XIII. p. 193; 1888), show that the Infusoria are not the only Protozoa possessing idioplasm in the form of idants. Not only are idants (chromatosomes) shown to exist in the form of loops, but their behaviour during karyokinesis is so accurately described as to leave no doubt that an 'equal division' is its outcome. The longitudinal splitting of the loops was observed not only in microscopic preparations, but in the living animal in the act of dividing. It is clear that *Euglypha* is well adapted for observation, and it would be of great value to investigate the relations of its nucleus during conjugation from the standpoint of this essay.

[2] Maupas, 'Le rajeunissement karyogamique chez les Ciliés.' Archives de Zool. expér. et gén. 2 sér. Vol. VII. Pl. IX. Figs. 1–14. Paris, 1890.

[3] R. Hertwig, 'Ueber die Conjugation d. Infusorien.' Munich, 1889.

[4] A micron or μ is the $\frac{1}{1000}$ of a millimetre.

yet compared the number of the idants in a micronucleus preparing for conjugation with the number in a micronucleus of an Infusorian in the act of fission; and the few figures which we possess, of either of these stages, afford us no reliable information on the point. The figures which Maupas gives of the micronucleus preparatory to conjugation in *Paramaecium caudatum* and *Onychodromus grandis*, lend support to my view, in so far as the number of idants is very large. In the first species I counted twenty-one in the half spindle which is figured, giving a total of about forty-two. But I will not lay too much stress on this point; the simplicity of my attempted explanation of the changes in the micronucleus appears to me to be strongly in favour of the view upon which the explanation is based.

If this assumption be well founded it provides a very simple solution of the problem of the complex divisions and repeated disintegrations of the micronucleus. *The first and second divisions are reducing divisions* which diminish the previously doubled idants to half the normal number, corresponding exactly to the 'reducing divisions' of sperm- and egg-mother-cell. *The third division, however*, which produces the two reproductive nuclei (male and female), from one of the four grand-daughter-nuclei of the micronucleus, *is an 'equal division,'* which causes each daughter-nucleus to contain as many idants as were possessed by the parent nucleus. This last division has no analogue in Metazoa, simply because their germ-cells are invariably either male or female, while the Infusorian micronucleus must give rise to both kinds of reproductive nuclei.

Three out of the four grand-daughter-nuclei of the micronucleus disappear, only one dividing to form the reproductive nuclei (*D* in the diagram, Fig. XII.). The fact that the others disintegrate can be understood in so far that they are superfluous and functionless, just like the polar cells of the animal egg. It is more difficult to explain why these three are always present, and still harder to find the true reason, the *causa efficiens*, of their disintegration.

With regard to this last question, an observation of Maupas may put us on the right road. He believes that he has observed that, of the four grand-daughter-nuclei derived from the micronucleus, the one which lies nearest to the bridge connecting the

two conjugating animals invariably gives rise to the reproductive nuclei. This is alone capable of further development, while the three which occupy more remote positions are destined to disintegrate and disappear. It is only the accident of position which fixes upon that one of the four which shall undergo development.

If this be true, the *causa efficiens* which decides upon that one of the grand-daughter-nuclei which shall give rise to the reproductive nuclei must be sought for in some influence which is exercised by the corresponding nucleus of the other animal, and which naturally affects most strongly that nucleus which lies nearest to it.

At any rate we are justified in assuming that the idioplasm of the four grand-daughter-nuclei of the micronucleus is, apart from individual differences, essentially similar, i. e. that each contains the same number of idants in the same stage of development, and this number will be half that which is normal for the species in question. Thus nine would be the number in *Urostyla grandis*, which would be reached in the following manner. According to my supposition, during the growth of the micronucleus from A^1 to A^2 (see Fig. XII), the 18 idants are doubled by longitudinal fission, becoming 36; the two following 'reducing divisions' not only diminish the idants from 36 to 18 in stage *B*, and from 18 to 9 in stage *C*, but lead to *a fresh grouping of the idants, just as in the analogous 'reducing divisions' of the egg- and sperm-cell.* Since the 18 idants are doubled, it is clear that each one of them will be represented by two idants in the enlarged micronucleus of stage A^2, and hence the two 'reducing divisions' can originate a number of different combinations of 9 idants, just as in the egg- and sperm-cell, described in the first part of this essay.

Although in any single individual, only four out of the numerous possible combinations would become actual, we may perhaps perceive,—in this very fact that there are always at least four different possibilities to select from,—the reason why all four grand-daughter-nuclei of the micronucleus are formed, and why both the daughter-nuclei undergo the second 'reducing division,' while the division of one of them alone would suffice to ensure the origin of two reproductive nuclei.

Objections.

It will be urged against my views that they are based upon a method of formation of the reproductive nuclei, which, although common among Infusoria, is by no means the only one. As a matter of fact, Maupas, whose researches form the only foundation for this part of my argument, describes another method in the *Oxytrichidae*. If I neglect the fact that in this case two micronuclei are found in the animal preparatory to conjugation, it is because this difference is merely due to the fact that two of the grand-daughter-nuclei (instead of only one) undergo a second division. Thus two pairs of reproductive nuclei arise, of which only one is functional, while the other disintegrates. But the theoretical explanation is in no way affected by these observations.

The only facts which do not at once harmonize with my view is the behaviour of the micronucleus in male *Vorticellidae*. In this case the period of growth of the micronucleus (stages A^1—A^2) is preceded by its division. I cannot at present explain this, unless it simply means that instead of four different combinations of idants out of which one functional reproductive nucleus is to be chosen, eight are in this case afforded. A glance at the figure given by Maupas (op. cit. p. 364) at once renders this suggestion clear. In any case, the extra division must be an 'equal division.'

Thus the departures from the ordinary modes of division of the micronucleus raise no definite objection to my explanation.

Evidence that the processes which I have explained as 'reducing divisions' are really such, is afforded by some of the figures given by Maupas, as in figs. 9–13 on Plate XVIII, in which the development of the spindle for the nuclear division of *Onychodromus grandis* is represented. The rod-like chromatosomes lie longitudinally in the spindle, and appear to be dividing transversely. Since we must imagine that the ids are arranged lengthwise, the transverse division of the idants must lead to a diminution in the number of ids in each rod to half their original number. Complete certainty cannot, however, be attained by an examination of these figures; the matter must be settled by fresh observations, especially directed to the point. The whole mechanism of nuclear division differs in essential

points from that of the Metazoa, so that without first making renewed investigations it is impossible to form a correct idea as to what should be regarded as a 'reducing division.'

According to my view, the explanation of the thrice-repeated division of the micronucleus consists, on the one hand, in the reduction of the number of idants and their arrangement in new combinations, and, on the other hand, in the differentiation of the two reproductive nuclei.

Those who agree with me in looking upon amphimixis as the union of idioplasms built up of ids from two individuals, will not hesitate to believe that the ids are reduced to half the normal number. It is impossible that there can, in this respect, be any difference between the amphimixis of unicellular organisms and that of Metazoa. It is not equally certain that my view of the production of fresh combinations of idioplasm by means of amphimixis can be proved in the Protozoa. It might be objected that it is useless for one Protozoon to possess the theoretical possibility of producing a great number of individual varieties of idioplasm, because each single animal is only able to utilize one out of many possible combinations. The two animals which commenced conjugation remain at the end of it, and there is no increase in number: hence the different nuclei which originated from the 'reducing divisions' cannot be divided among different animals, as is possible in the case of the four sperm-cells which are formed by one sperm-mother-cell, and which contain four different combinations of idants.

This objection is easily met, for exactly the same thing happens in the development of the ova in Metazoa. Just as only a single egg, with a single combination of idants, can proceed from each egg-mother-cell, while the other three combinations disappear in the polar cells,—so, in this case, three grand-daughter-nuclei of the micronucleus disappear, and one only persists. The process receives a meaning when we remember that countless numbers of egg-mother-cells, containing precisely similar combinations of idants, are destroyed by the process of arranging the idants in fresh groups. *The same explanation holds among Infusoria; for here also countless individuals contain precisely similar combinations,* this being true of all individuals which are derived from either of the animals proceeding from any one conjugation. Just as the collective

egg-cells of a mother would contain identical germ-plasm, if they did not undergo the 'reducing divisions' before reaching maturity,—so all the descendants of an Infusorian after conjugation would contain similar combinations of idants, if the repeated 'reducing divisions' did not precede the formation of the reproductive nuclei.

Variety of individual character in the hereditary substance is thus brought about by means of these divisions.

The Deeper Significance of Conjugation.

No one will attempt to oppose the view that the deeper meaning of conjugation is closely connected with that of sexual reproduction. The process is, in both cases, that of nuclear fusion, and, in fact, the formation of a complete nucleus by the union of two 'half-nuclei,' as they may be called, that is, two nuclei which contain only half the normal amount of hereditary substance or idioplasm, and only half the normal number of individual hereditary units or ids. From this fusion a new nucleus is formed which contains that amount of hereditary substance and that number of ids which are normal to the species. This is my explanation of the process of fertilization in the Metazoa, an explanation which I can extend to the Protozoa, now that the long looked for and, indeed, partially observed nuclear fusions accompanying conjugation have been proved by Maupas to be actual facts. Those who do not accept my theory of ids can only maintain that the nuclear fusion of conjugation and fertilization leads to the formation of a new nucleus by the fusion of two equal masses of individually distinct hereditary substance or idioplasm.

The view which I expressed in 1873, and which has since then been established by Strasburger, O. Hertwig, and myself, of the essential similarity of the male and female sexual cells, can now be confidently extended to conjugation; for Maupas has already acknowledged the two reproductive nuclei to be essentially similar. They certainly are so, inasmuch as they exhibit no traces of the fundamental antagonism which has been spoken of as a 'male and female principle' in the egg- and sperm-cell.

If we may now assume that the nuclear substance which

arises in the same way in Infusoria and Metazoa bears a similar significance in both, we may then proceed to the conclusion set forth above that conjugation and fertilization are both essentially concerned with the mingling of the *hereditary tendencies of two individuals.*

At the time when I developed this view, which sought the ultimate meaning and true cause of the existence of sexual reproduction in the continual supply of fresh combinations of hereditary tendencies, I contrasted the Metazoa and Metaphyta on the one hand with the Protozoa and Protophyta on the other, and maintained that the chief sources of variability in the former, the multicellular beings, viz. the external influences (including the effects of use and disuse) which alter the body, can have no influence on the processes of selection which alter the species, because their effects are somatogenic and as such cannot be inherited. Only those predispositions can be inherited which are contained in the germ-plasm, but these are either entirely uninfluenced by external agencies, or, if altered at all, only very rarely in the same direction as that taken by the somatogenic changes which follow the same cause. Although I naturally did not assume that the germ-plasm itself was entirely unchanged by external influences, the extraordinary persistence of heredity taught me that the change was small and could only take place by imperceptibly small steps. Such causes might well have been the source of the gradual uniform changes in *all* individuals of a species, if the latter were subjected to the same modifying influences during long series of generations, but not the source of the countless individual differences, ever-varying in direction. This protean individual variability is the indispensable preliminary to all processes of selection, and the unceasing mingling of individual hereditary tendencies, which is brought about by sexual reproduction, was in my opinion the source of this variability. I am now, if possible, more firmly convinced than ever of the soundness of this view, and I wish to extend it in one direction.

At the time I have been speaking of, I looked upon unicellular beings as organisms in which external influences could directly call forth hereditary changes; for in them reproduction involved the fission of the cell so that changes undergone by the latter must be transmissible to either half. As an example,

I selected a Moneron as defined by Häckel, viz. an organism without a nucleus. I purposely abstained from considering those unicellular beings which possess nuclei, because I was then only concerned with bringing forward the general conception that sexual reproduction exists in order to ensure individual variability. I was, however, well aware that in the nucleated Protozoa, and especially in those Infusoria, which although unicellular are extremely highly differentiated, such a simple transmission of acquired peculiarities was hardly conceivable. Now that we possess accurate knowledge of the most essential points in the process of conjugation, it is possible to approach this problem somewhat more closely.

The fact, as we now know it, that conjugation in Infusoria is a mingling of the nuclear substances of two individuals, permits the conclusion that, in these animals, the whole individuality of the cell, and thus of the cell-body, is contained in the nuclear material as predispositions or hereditary tendencies, just in the same manner as has been proved in the case of the germ-cells of the Metazoa. Nussbaum's experiments upon the artificial fission of Infusoria, and those which Gruber undertook at my suggestion in the Zoological Institute at Freiburg, prove that the nucleus determines the regeneration of the mutilated animal, and that it contains, in some way, the essence of the whole organism in all its details. Hence we must believe that all those variations which appear in Infusoria, in consequence of external influences, can only pass on to the products of fission *when they are accompanied by corresponding changes of the nuclear substance*; or, in other words, we come to the conclusion that the hereditary transmission of *somatogenic* changes does not, as a rule, take place, or only does so when they are accompanied by corresponding *blastogenic* changes. The use of both these expressions only implies a correspondence, and not a similarity of application, the 'soma' of Metazoa corresponding to the cell-body of Infusoria, the 'germ' to the nuclear substance. The broken bristles of an Infusorian are renewed in the products of fission because the predisposition to form them is contained in the nuclear substance. Mutilation is no more hereditary here than in the Metazoa. Furthermore, all changes in the cell-body of an Infusorian are not accompanied by corresponding changes in the nuclear substance, and all cannot therefore be inherited;

not only is this the case but it seems very questionable whether the changes originated by use and disuse are in any way more hereditary than they are in Metazoa. There are no direct observations to test whether any of the cilia in an Infusorian could be strengthened by increased use, either in connexion with some new kind of food, or with a struggle against stronger currents in water; but we need not doubt that in these organisms, small and relatively simple as they are, functional hypertrophy and atrophy play the same rôle as in larger and more complex beings. I would refer my readers to Wilhelm Roux's excellent treatise on this subject in the higher organisms. If certain cilia in an Infusorian were to increase in size as the result of more active function, how can we conceive the transmission of this change to the hereditary substance contained in the nucleus? The path is certainly shorter than that from the human brain and finger muscles to the reproductive cells; but distance, like all measurements, is only a relative idea, and the question arises whether there is any ground for the assumption that such increased growth in the cilia causes any *corresponding* change in the nuclear substance of the animal. But if this does not occur, any inheritance of acquired characters is as impossible as it is in man. How, for instance, can an increase of the adoral ciliated zone of a *Stentor* be transmitted to both the products of its fission, considering that the hindmost of these has to form an entirely new mouth? It might perhaps be pointed out that R. Hertwig believes he has seen the mouth of the hinder offspring arise by budding from that of the anterior; but the artificial division of *Stentor*, as effected by Gruber, proves that the mouth of the posterior part is not dependent on the existence of the original mouth, but can arise quite independently, provided only that a portion of the nucleus is present.

I therefore hold that *a belief in the inheritance of acquired characters by the highly differentiated Protozoa, as well as by Metazoa, must be opposed*, and I imagine that *the phyletic modifications of Protozoa arise from the germ-plasm, that is from the idioplasm of the nucleus.*

We can now understand why nature has laid so much stress on the periodical mingling of the nuclear substances of two individuals,—why she has introduced amphimixis among these

animals. Clearly it has arisen from the necessity of providing the process of natural selection with a continually changing material, by the combinations of individual characters.

Amphimixis in all Unicellular Organisms.

We may extend this conception and enquire whether it may not, in reality, apply to all unicellular organisms, that is all which possess a nucleus and cell-body. The conclusion can scarcely be avoided if it be admitted that the nucleus invariably bears the same essential significance, and this can hardly be doubted. If, as a matter of fact, the lowest, apparently structureless unicellular organisms contain a nuclear substance which dominates and controls the entire animal, it follows that all lasting and therefore hereditary variations of both cell-body and nucleus must proceed from the latter, while those direct changes of the cell-body which are produced by external influences, are as incapable of hereditary transmission as the mutilation of the body of an Infusorian. Thus changes in the molecular constitution of the cell-body, such as we might imagine to be the result of the exercise of particular functions (for example, the more powerful movements of an amoeba) would probably be transmitted to the immediate offspring, but would disappear with the cessation of those causes which rendered necessary the increased exercise of the function concerned.

My earlier views on unicellular organisms as the source of individual differences, in the sense that each change called forth in them by external influences, or by use and disuse, was supposed to be hereditary, must therefore be dismissed to some stage less distant from the origin of life. I now believe that such reactions under external influences can only obtain in the lowest organisms which are without any distinction between nucleus and cell-body. All variations which have arisen in them, by the operation of any causes whatever, must be inherited, and their hereditary individual variability is due to the direct influence of the external world. Loss of substance must not however be included among such individual variations: repair would take place by regeneration in these simplest forms of life just as in higher Protozoa. At least, I think this is not contradicted by the fact that the molecular structure of such a Moneron, although without the guidance of a nucleus, retains

a certain external form and limit of size, which it will regain after being mutilated. Growth and division are themselves the outcome of such tendencies implanted in the molecular structure: this, for example, is the case in Bacteria. The whole question comes to an end when we reach those lowest of all beings, which are entirely formless and have no fixed size,—beings which we must regard, little as we know about them, as crossing the very threshold of organic life [1].

It is interesting to observe that, from this point of view, the nucleus presents itself in a new light. By the agency of conjugation and fertilization it becomes *an organ for maintaining the constant renewal and transformation of hereditary individual variability*. Besides this, it plays the part of protecting the species from the too powerful effect of transforming external influences upon the body, inasmuch as it tends to prevent these from becoming hereditary, not indeed actively, but simply because every external influence does not cause a corresponding alteration in the nuclear substance, and thus the latter containing the older predispositions tends to restore, after each fission, the older condition of the cell-body. It simultaneously acts as a conserving and as a progressive principle, exactly as the sexual cells of higher beings are, according to my views, supposed to behave. The reproductive cells exert a conserving force, inasmuch as they retain, with incredible tenacity, the hereditary tendencies contained within them, and, above all, because they are unaffected by those changes in the soma which are brought about by external influences: but they also act progressively by means of amphimixis and the consequent periodical mingling of the hereditary predispositions of two germ-cells, one from each parent, which as we have seen, takes place by the removal of half of these predispositions and by the arrangement of those which remain in fresh combinations.

If I am correct in my view of the meaning of conjugation as a method of amphimixis, we must believe that all unicellular organisms possess it, and that it will be found in numerous low organisms, in which it has not yet been observed. But it is by no means safe to make the *a priori* assumption that conjugation

[1] Nägeli, 'Mechanisch-physiologische Theorie der Abstammungslehre.' Munich, 1884.

may not also take place in the form of a fusion of two individuals among the non-nucleated animals, the Monera: and it may be precisely here that a fusion of two whole animals with a view to the mingling of characters was first effected. We are acquainted with a form of conjugation in certain of the *Bacillariaceae*, and even if it is not absolutely certain that the species in question, *Cocconeis pediculus*, is without a nucleus, many details of the process indicate that the whole mass of the organism contains the conjugating idioplasm: this is chiefly suggested by the minute size of the conjugating individuals, which invites comparison with the nucleus, diminished by 'reducing divisions,' in order to facilitate amphimixis. For this reason I believe that we ought not to follow Maupas in constructing a general definition of conjugation as the fusion of nuclei.

The Theories of Rejuvenescence and of Mingling.

I hold that the deeper significance of every form of amphimixis,—whether occurring in conjugation, fertilization, or in any other way,—consists in the creation of that hereditary individual variability which is requisite for the operation of the process of selection, and which arises from the periodical mingling of two individually different hereditary substances.

That such a mingling is the immediate result of amphimixis is no longer open to dispute, and perhaps at no distant date it will be admitted that the variability I have spoken of must follow as a direct consequence. It is well known, however, that many and indeed the majority of scientific men, who have expressed themselves on the point, hold the opinion that this mingling of two hereditary substances is not the one object of amphimixis, —its ultimate and most important consequence, and does not explain the reason why it was introduced into the organic world. It is obvious that my view as to the effect of amphimixis in originating variability may be perfectly correct, without the essence of fertilization or of conjugation being thereby explained. What I regard as its chief object may after all only be secondary, and the true significance of the process may lie in some consequence unknown to me or which I have overlooked.

We know that, up to the present time, fertilization has been regarded as a vitalizing process, without which the development of the egg either cannot occur at all, or only exceptionally. I need not repeat what I have already said upon this idea in the first part of the essay, and it is not necessary to follow the gradual modifications which have been introduced; but I should like to submit to a trial the support which the upholders of these views have always sought in the process of conjugation, and which they are still seeking to-day.

Maupas, the able investigator of the vital processes of Infusoria, considers that the effect of conjugation is such as to ensure the continuation of the species; it imparts to the animal the power 'de renouveler et rajeunir les sources de la vie.' Hence, according to this view, the most profound significance of conjugation is to be found in rejuvenescence, an idea which was long ago accepted and applied, sometimes to fertilization, sometimes to conjugation, and sometimes to both together, by Bütschli, Engelmann, Hensen, E. van Beneden, and more recently by R. Hertwig. Maupas also looks upon these two processes as essentially similar, and regards both as a 'rejuvenescence,' without which life would, sooner or later, come to an end. He sharply distinguishes between this somewhat mystical rejuvenescence and that which consists in the renewal of many of the external parts of the animal, such as mouth, bristles, cilia, &c. Such regeneration is certainly connected with conjugation, but it also occurs at every fission of an Infusorian and cannot therefore be an essential part of the former process. The rejuvenescence which Maupas regards as the essence of conjugation is something entirely different, and can hardly be described except as a 'renewal of vital force,' using the expression in the sense of the old natural philosophers. All other attempted definitions of this rejuvenescence are vague and unsatisfactory. It may well be doubted whether the return to a certain form of 'vital force' is in harmony with the physiology of to-day. On the other hand, no period of time has been entirely without an advocate of this principle, and quite recently the accomplished physiologist Bunge has, although with much reserve, again supported the ancient belief in a vital force. In any case we could only accept this idea if it were shown that there is no chance of explaining the phenomena of life, even in principle,

without such acceptance. Bunge[1] is certainly correct in maintaining that we are not at present in a position to completely explain any of the simple processes of life from known chemical and physical forces; but it by no means follows that they are inexplicable by such means. All we can say is, that everything that we do know about natural processes tells against the rejuvenescence of life by conjugation believed in by Maupas, as I have already pointed out in an earlier essay. To my mind it is difficult to understand how an almost exhausted vital force could be raised again to its original state of activity, as the consequence of a union with another equally exhausted force. Maupas can only reply that we do not understand the essence of any 'phénomène primordial'; but if we cannot follow all the details of the chemical processes which for example bring about the phenomena of assimilation, because they are so extremely complex, and do not admit of our tracing the changes which succeed each other through the rapidly shifting stages—because this is so, we do not therefore take refuge in the assumption that the whole process is unintelligible. But this, in my opinion, is the case with the 'rajeunissement karyogamique' of which we know neither the beginning—the exhausted condition of the vital force, nor the end—the rejuvenescence, nor any intermediate stage. The whole conception is simply a fancy, the outcome of earlier deeply rooted convictions as to the necessity of death and the 'vitalizing' influence of fertilization. I do not care, however, to base my opposition to Maupas' views on the rejection, as fundamentally untenable, of the theory of rejuvenescence; the argument is superfluous.

In considering *how it is that amphimixis has come to be regarded as a renewal or rejuvenescence of vital force*, the question naturally arises—why are we not content to see in this union of two nuclei, that which observation shows to us, viz. the union of two nuclear substances, and hence the mingling of two individually different hereditary predispositions? Maupas himself admits that this occurs, and indeed allows that variability is favoured thereby, thus supplying the necessary material for processes of selection. Why are we not content with this explanation, why do we seek for something further?

[1] Gustav Bunge, 'Vitalismus und Mechanismus'; ein Vortrag. Leipzig, 1886.

Obviously for no other reason but that we are saturated with the old notion that the egg cannot develope without fertilization, that fertilization is the same as vitalization. But was not this view overthrown long ago by facts? Are we not aware that, under certain circumstances, the egg can develope without fertilization? And is not this often true, for example in the Bee and in *Apus*, of that very egg which is also capable of fertilization? No one would have regarded fertilization as the vitalizing of the egg if the great majority of ova had developed parthenogenetically, or if science had first become acquainted with parthenogenesis and, later on, with fertilization. We should then have said that there must be some advantage in the mingling of two hereditary tendencies which has led to the introduction of amphimixis. But the facts are otherwise,—for centuries mankind has recognized this mingling as the indispensable antecedent to the development of offspring, and now, when we find that, under certain circumstances, an egg can develope without fertilization, we are unable to get rid of the old prejudice in favour of the view that the mingling is something more than a mere preliminary to development,—that it is an accessory force which bears some special and entirely peculiar significance. We cling to some supposed after-effect of the vitalizing influence of fertilization, extending through many generations, and against such an illogical theory even facts fight in vain, for the number of generations through which this after-effect is supposed to extend, is entirely dependent on the will of the controversialist, and keeps pace with the increasing length of the observed series of parthenogenetic generations. Maupas himself finds the number of such generations, which may succeed each other in some 'rare' species of Crustacea and Insecta, entirely insufficient to justify the conclusion that these agamic generations can continue indefinitely. I certainly believe that in most cases they are not of unlimited duration, because nature has chiefly fitted them for a cyclical method of reproduction,—for a regular alternation of parthenogenetic with sexual increase. But there are species like *Cypris reptans* which I have investigated (see Part II of this essay), in which it is certain that no such cycle exists, and that parthenogenesis continues without interruption. I have observed about forty generations in the case of *Cypris*

reptans: this is not an unending series, but we do not know of any reproductive cycle which, after forty agamic generations, returns to a sexual one. So far as the argument is concerned, it does not signify at all whether such cases are rare, as Maupas thinks, or common: even their entire failure would afford no proof of the theory of rejuvenescence. For the theory of mingling,—if I may so designate my hypothesis,—is founded on the species-preserving influence of amphimixis, and leads us to expect that, wherever it is possible, nature will always introduce amphimixis into the reproductive history of a species and will render its employment obligatory. We should have no ground for wonder if purely agamic reproduction had no real existence. The vitalizing influence of amphimixis would not be proved even if this were the case.

On the other hand, I think a single example of continuous agamic reproduction proves that amphimixis is not absolutely necessary for the unlimited duration of life.

But if amphimixis is not absolutely necessary, the rarity of purely parthenogenetic reproduction shows that it must have a wide-spread and deep significance. Its benefits are not to be sought in the single individual; for organisms can arise by agamic methods, without thereby suffering any loss of vital energy: amphimixis must rather be advantageous for the maintenance and modification of species. As soon as we admit that amphimixis confers some such benefits, it is clear that the latter must be augmented as the method appears more frequently in the course of generations; hence we are led to enquire, *how nature can best have undertaken to give this amphimixis the widest possible range in the organic world.*

The following is an attempt to supply an answer to the question. The increase by means of budding and fission would be retained in multicellular plants and animals, on account of its great advantages, but it would only endure for a shorter or longer series of generations. Moreover, the expected advent of amphimixis would only take place when the collective hereditary tendencies of the individual are concentrated in the nucleus of a single cell; hence the mechanism of reproduction must have been associated with unicellular germs, and amphimixis became bound up with reproduction. I cannot remember that it has ever been

maintained that the ontogeny of Metazoa and, so far as I am aware, of Metaphyta also, primarily depends on the necessity for sexual reproduction, or, better still, on the existence of *unicellular germs*. An ontogeny must then follow; for the collective hereditary tendencies of an animal being concentrated in a single cell, they must therefore, during development, pass through a series of stages very similar to those of their phyletic history. But, besides the germs destined for sexual reproduction, there are other unicellular germs, spores, &c.; and hence it is clear that the unicellular condition brings other advantages than those which amphimixis confers; but these unicellular agamic germs never exhibit any approach to the extent of range witnessed in sexual cells, and the origin and universal existence of unicellular germs are therefore to be sought in the latter.

I have already shown that the sexual cells, upon their first appearance, in some simple cell-colony such as *Pandorina*, would be compelled to undergo a nuclear 'reducing division,' after a relatively small number of sexually reproduced generations; because otherwise a continued doubling of the nuclear units must have occurred in consequence of the periodically repeated union of the nuclear substance of different individuals. This 'reducing division,' which is now securely proved for both male and female sexual cells in Metazoa, has, however, another meaning.

I proceed from the assumption that nature aims at the widest possible range for amphimixis. *How could this be obtained more effectually than by rendering the unicellular germs incapable of developing alone?*

The male germ-cells, being specially adapted for seeking and entering the ovum, are, as a rule, so ill provided with nutriment that their unaided development into an individual would be impossible; but with the ovum it is otherwise, and accordingly the 'reducing division' removes half the germ-plasm, and the power of developing is withdrawn.

What happens in the unicellular organisms? Here also our theory demands that periodic amphimixis should be provided by nature. For the attainment of this object it was indispensable that, as in Metazoa and Metaphyta, the organisms should, at certain periods, arrange themselves in pairs, and that their

nuclei should be in the state best adapted for fusion,—viz. that the mass should be diminished so far as to reduce the hereditary units, or ids, to half. And all this as a matter of fact takes place. But it is nevertheless insufficient to ensure the desired result; for Maupas' experiments show us that, in spite of it, conjugation may be absent. The impulses which induce Infusoria to seek one another, and to pair, appear at certain periods and under certain external conditions, but if the latter are not favourable the impulses are not manifested and after the lapse of some time the power of conjugation is completely lost in the colony in question. I assume that Maupas' observations are correct, and am not criticizing them; but his own results prove, in my opinion, that his interpretations are erroneous in so far as he endeavours to find support for the theory of rejuvenescence by means of the facts which he has observed. Those colonies which have passed the proper time for conjugation gradually die out. Maupas considers that they die *a 'natural' death* in consequence of *old age*. He claims to have proved the occurrence of 'physiological' death in unicellular organisms, and to have refuted my views as to their potential immortality.

But I believe that the facts brought forward by him are capable of a different and a more correct interpretation.

What happens when a colony has passed the appropriate period and has therefore lost the power of conjugation? The very same thing which happens to the ovum which has attained maturity and has extruded its polar bodies — *disintegration, preceded by the loss of all power of development.* I believe that this result proceeds from the same cause in both cases,—*the reduction of nuclear substance*, i. e. in the Infusorian, the substance of the micronucleus. The egg disintegrates because the nuclear substance is insufficient for the commencement of ontogeny, and is imperfectly adapted for its preservation; the Infusorian disintegrates because its macronucleus must be renewed periodically, and because this cannot occur after the micronucleus has perished. And Maupas informs us that the latter disintegrates sooner or later, if the proper time for conjugation has passed by.

If we ask, how is it that the micronucleus disappears when conjugation is excluded, Maupas answers that the necessary

rejuvenescence being absent, the animal grows old (sénescence) and finally dies *a natural death*. I do not agree with this interpretation. The significant inner changes which take place during conjugation were obviously prepared some time beforehand, and the micro- and macronuclei of animals which feel impelled to conjugate are already in a state which must sooner or later lead to profound changes of one or both—and this whether conjugation has taken place or not. In either case these changes will be essentially the same,—the destruction of the macro- and division of the micronucleus. One thing alone does not happen,—the coalescence with the nucleus of another individual. But we know that all the products of the micronuclear division disappear except that which gives rise to the reproductive nuclei and that this is always the one lying nearest the connecting bridge which unites the conjugating animals. If then it is the influence of another animal which renders a grand-daughter-nucleus capable of further development, we are led to conclude that such an influence is lost when conjugation does not occur. In this, I believe, lies the cause which leads the vital energies to grow weaker and finally to cease, in the descendants of an animal which has undergone the changes described above. It is the same with the ovum,—the processes of maturation which prepare for fertilization, produce changes which prevent the future life of the egg-cell, unless it be fertilized.

Maupas will reply that it has not yet been proved that such changes appear when conjugation is absent: he has never observed them in the Infusoria which he prevented from conjugating. He did not make the observation because he regarded the changes as phenomena of age. It now remains to follow accurately the alterations which appear in the macro- and micronuclei, when a colony has been prevented from conjugating. The observations will be difficult, because they must extend over many generations; for the end of the period favourable for conjugation cannot be foretold with certainty and, according to Maupas, is not reached in all the animals of a colony at the same time.

My interpretation does not by any means require that the changes in animals prevented from conjugating, should follow precisely the same course and pass through exactly the same

stages as those which occur in conjugated animals. This is *a priori* very improbable. We must not forget that the interval between two successive conjugations extends over many generations, and that those inner conditions which prepare for conjugation are gradually built up, reach their highest point, and are then lost. If, when the appropriate period has arrived, conjugation takes place, the long-prepared processes of maturation take their normal course; but if this period is passed by, the whole future development *is abnormal.* The animal increases a hundredfold or more, but development cannot pursue its normal course, the nucleus degenerates,—sometimes the macronucleus being the first, sometimes the micronucleus,—and finally neither assimilation, nor the maintenance of the characteristic body-form can be kept up, and the animals die one after the other. The irregularity in the course of these phenomena, as Maupas describes them, points to the fact that we are concerned with an abnormal process.

Does Natural Death occur in Unicellular Organisms?

Why do some writers regard the process described above as the equivalent of the normal death of Metazoa? Merely because of the traditional dogma which asserts the necessity of normal 'physiological' death. They overlook the fact that *in Infusoria conjugation is a normal process*, the periodical recurrence of which is provided for by nature, and upon which the whole vital mechanism of these animals is, to a certain extent, regulated. Nature must have amphimixis, and brings it about by the internal changes which impel the animals to pair, and by those which gradually render them unable to live when conjugation is artificially prevented. It is, as I have already argued, precisely equivalent to the effects which follow the non-occurrence of fertilization. The spermatozoon which fails to find an ovum, dies. If anyone finds pleasure in bringing confusion into ideas which have just become to some extent clear, he may speak of this as the 'normal death' of the spermatozoon; I call it an accidental death, although I am well aware that this unhappy accident is far more common than the successful attainment of the normal object of a spermatozoon's life. In most animals millions of spermatozoa are lost before a single

one attains its object; and these vast numbers are necessary just because the way to the egg is so very precarious. Must we regard this destruction as normal because it is so common? Is not fertilization the normal aim of the vital processes of the spermatozoon? And does not the destruction of those numerous spermatozoa which have missed their aim result from the fact that they are not adapted for a long independent life,—that their vital force is soon expended because no precaution has been taken to renew it by food? But has this lack of food been brought about because it *could* not have been taken however desirable it may have been? I believe that spermatozoa want a mouth, and all other adaptations for the absorption of nutriment, because they do not need them for the attainment of the object for which they exist, and that, were it otherwise, they would have been adapted for living longer. Useless adaptations are never met with. Spermatozoa gone astray are of no further value to the species, and they may just as well disappear. And so it is with those Infusoria which have failed to conjugate; they are useless to the species, since its maintenance requires the periodical crossing of individuals and of this they are no longer capable. If Infusoria were not adapted for this crossing they could live on for ever without amphimixis, just as a parthenogenetic egg and its products live on without it. But those very changes which make an Infusorian capable of conjugation remove all possibility of unending life without it, just as the two 'reducing divisions' withdraw this possibility from the egg. An even closer parallel can be drawn, for Kupffer and Böhm[1] have shown, by the case of *Petromyzon*, that there are animal eggs which only undergo the *first* polar division before they come in contact with the spermatozoon, the second following after it has penetrated. Such eggs when unfertilized, contain the quantity of germ-plasm required for embryogeny, but are, nevertheless, incapable of parthenogenetic development. We cannot at present recognize those intimate changes upon which this incapability must depend, but we may conclude that it is a consequence of changes preparatory to amphimixis. The eggs are so completely adapted for this event that their power

[1] Böhm 'Ueber die Befruchtung des Neunaugen-Eies.' Sitzgsber. d. math.-phys. Klasse d. bayr. Akad. d. Wissensch., Munich, 1887.

of independent development is interfered with by the preliminary changes. But, just as eggs, in which these internal changes have once been carried out, cannot remain indefinitely thus prepared, but very soon change so that they are no longer adapted for fertilization, and finally decay,—so it is with an Infusorian which has passed the time for conjugation ; it becomes incapable of conjugating, and finally, of living.

As far as I can see there is only one point of view from which the gradual dissolution of an Infusorian which has not succeeded in conjugating can be rightly regarded as a kind of natural death ; viz. if we could prove *that its destruction is dependent on some adaptation especially directed to this end.* Maupas is, naturally enough, very far from accepting this point of view ; for he clings to the old belief that death is a universal attribute of life, and is not a phenomenon of adaptation. From my standpoint we might argue as follows :—Conjugation must take place periodically because the crossing of individuals is necessary for the maintenance and development of the species. If it was impossible to ensure the occurrence of crossing in all or the great majority of individuals and colonies, there would be a danger of the uncrossed ones getting the upper hand. To prevent this, the animals which do not conjugate must be prevented from living on indefinitely, in fact natural death must occur, and this was ensured by conferring upon the macronucleus of the animal such a structure that it was used up during assimilation, while the micronucleus was so constructed that it underwent dissolution in consequence of the divisions preparatory to amphimixis, or as we may otherwise imagine it.

I know of no biological principles which are antagonistic to such a view, but I scarcely believe that it is a correct one ; analogy with the sexual cells is against it. I do not doubt that nature would be quite capable of bringing about a natural death for those animals which have escaped conjugation, if it were necessary for the maintenance of the species ; but their destruction does not appear to be necessary. We should hardly maintain that the dissolution of a spermatozoon which has missed its mark is dependent on the appearance of natural death, especially designed for it. On the contrary, it is obviously destroyed simply because the vital conditions necessary for its continued existence are wanting, viz. fusion with an

ovum. The latter also dies for a similar reason when it has not been fertilized. Some years ago I described the different manner in which the eggs of two closely allied species of Crustacea behave when they have no prospect of being fertilized [1]. If a female of *Moina paradoxa*, bearing winter-eggs in the ovary, be separated from the males, it nevertheless deposits its ova in the brood-chamber, but they utterly disintegrate in a few hours and are washed away by the water as it flows through the chamber. It is very different with *Moina rectirostris*; the winter-egg, when ripe and ready to pass into the brood-chamber, almost occupies the entire ovary. When males are absent and fertilization does not occur, the egg is not laid but is retained by the isolated female in her ovary in which it remains apparently unchanged for many days, probably quite capable of being fertilized. Finally it changes in appearance, losing its uniform finely granular look, while the fat-globules and particles of albumen fuse together into great irregular masses which are presently rather rapidly reabsorbed. Instead of winter-eggs the parthenogenetic summer-eggs are now formed, and we may maintain that the material of the former is not lost to the individual or to the species when fertilization is excluded, but is converted into new ova which do not require fertilization. No one can doubt that the habit of laying the winter-egg only after the stimulus provided by fertilization, is an adaptation; but who would explain in this manner the destruction of the unfertilized egg, which remains in the ovary? This destruction is certainly not purposeless; but there are cases of unintended usefulness, and other species of *Moina* prove that this is one of them, for the unfertilized eggs are destroyed in the brood-chamber (where their material *is* lost). The destruction is therefore no adaptation but merely a consequence of the constitution of the egg which is so altered by preparation for the fertilization which should have ensued, that it can neither develope into an embryo nor continue to live. It is just the same, if I mistake not, with Infusoria; the gradual destruction of those animals which do not conjugate is no special adaptation, but rather an inevitable consequence of the necessary internal

[1] Weismann, 'Beiträge zur Naturgeschichte der Daphnoiden,' Leipzig, 1876–79. Abhandlung IV. 'Ueber den Einfluss der Begattung auf die Erzeugung von Wintereiern.'

changes which lead to conjugation, which could perhaps only have been prevented by special means [1].

Therefore we cannot speak of natural death as an adaptation to prevent unconjugated individuals from gaining the upper hand; and in any case natural death cannot be admitted to obtain among Infusoria *in general*, inasmuch as it only occurs in *those animals which are abnormal in not attaining to conjugation.*

We need not discuss whether the dying out of the unconjugated animals in an Infusorian colony, is an adaptation, specially intended for the removal of these harmful individuals, or whether, as I prefer to assume, it follows as a consequence of those changes which are preparatory to pairing. But even the former assumption affords no support to Maupas; because the natural death presupposed by him is the very reverse of an adaptation, being a fundamental attribute of life itself,—the inherent tendency to wear itself out. According to this view, Infusoria are predestined to death; they can however be rescued by the magic of conjugation, and thus acquire a new span of life.

Such a view does not admit of direct refutation; we can only show *that it has its origin in the old mystic conception of life, and that it is superfluous.*

Conjugation was long spoken of as the 'sexual reproduction' of Infusoria before we had a more intimate knowledge of the nature of the process. The '*tertium comparationis*' was that fusion of two cells into one which occurs at any rate in the original form of both fertilization and conjugation. I have been accustomed for many years to urge, in my lectures, that conjugation is not reproduction, but rather its opposite; for reproduction implies an increase of at least one in the number of individuals, while conjugation leads to a decrease, two individuals fusing into one. It has long been recognized that the processes which take place in conjugation and fertilization *have in themselves nothing to do with reproduction.* Maupas admits this and expresses it quite clearly and correctly when he states that

[1] I am here referring to the interesting facts discovered by R. Hertwig, which he explained as an Infusorian parthenogenesis. The subject is not, however, sufficiently mature for further consideration in this place. See R. Hertwig, 'Ueber die Conjugation der Infusorien.' Munich, 1889.

fertilization in the Metazoa is always associated with reproduction, but that the one process is not necessarily an accompaniment of the other, and that, as a matter of fact, the conjugation of Infusoria has nothing to do with reproduction. The majority of previous writers believed that conjugation revived the exhausted power of multiplying by fission. Maupas shows that this is not the case, that not only is fission deferred for a comparatively long time after the occurrence of conjugation, but that animals which have been prevented from conjugating continue to divide for a considerable period.

The view which Maupas thus overthrows was never a legitimate inference from accurate scientific observations, but was one of those traditional conceptions which gain acceptance after having been consciously or unconsciously derived from other similar conceptions. The supposed vitalizing force of fertilization was looked upon, for a long period of time, as the condition of all development and reproduction. The opposing facts were not at first strong enough to shake the foundation of this idea, and the preconceived notion that the magic of fertilization was the sole vitalizing life-maintaining principle, endured, while the facts of asexual and parthenogenetic reproduction were, by some evasion or other—the influence of fertilization extending over many generations, &c.—forced into the Procrustean bed of the received fundamental conceptions.

Even Maupas remains half buried in these old ideas. Although he has rightly recognized that fertilization and reproduction are two entirely different and even antagonistic processes, that they may be connected, as in the Metazoa, or disconnected, as in the Protozoa, he still holds to the old view of the vitalizing influence of amphimixis; he speaks of it as a 'rajeunissement karyogamique,' and declares it to be a means for the kindling afresh of that life which would, without it, waste away into death. He quite forgets that this view wholly depends upon the facts of fertilization among Metazoa, viz. in the inseparable connection between fertilization and reproduction which we find in these animals, but which *he himself has shown to be absent from the Protozoa.* He overlooks the consequence of this absence, viz. the proof that in this case '*post hoc*' is not '*propter hoc*,' and keeps to the old standpoint which was a right one only so long as we were obliged to believe that new

life could not arise without amphimixis, i. e. that reproduction was always associated with fertilization.

As I have already said, I regard the power of living on indefinitely when the vital processes have once begun, as the fundamental peculiarity of living matter. But this principle fails in so many organisms that its very existence was, for a long time, entirely overlooked, and hence the limited duration of life, together with its termination in natural death, were regarded as laws dominating all living beings. Undoubtedly the capability of unending life has been lost in very many organisms of greater or less complexity, and it is, I think, interesting to trace the causes which have led to this loss, and have rendered it necessary and even advantageous.

I will very briefly recall the manner in which the mortality of Metazoa may be explained, for this has been treated in earlier essays, and my views on the point have undergone no essential change. The immortality of Protozoa was carried over to the germ-cells of Metazoa and Metaphyta whether they are sexual, i. e. adapted for amphimixis, or not. In either case they posses potential immortality, i. e. they can, under the conditions imposed upon them by their constitution, continue without limit to exhibit the phenomena of life. The conditions under which the sexually differentiated germ-cells live include the fusion of two in amphimixis, but it is not generally included among the conditions imposed upon agamic or parthenogenetic germ-cells, and, when imposed, it only requires to be fulfilled again after the lapse of a certain period.

I will not repeat the reasons which, I believe, explain why the Metazoan soma has been permitted to lose, or has been compelled to lose, the power of unending life, and why natural death has made its appearance. I will only call to mind *the fact that, according to the principle of panmixia, every faculty must disappear as soon as it ceases to be necessary.* As soon as differentiation into soma and germ-cells,—viz. the formation of Metazoa and Metaphyta,—took place, this principle began to act, for the species could be maintained without the immortality of single individuals. Whether this immortality is in any way compatible with the high differentiation of the Metazoan body, and if so, whether it would be useful, are questions

which may remain unanswered—it is enough that it was unnecessary.

In Protozoa unending life was an inevitable necessity for the maintenance of the species.

Potential immortality is found from the very lowest organisms to the higher Protozoa and to the germ-cells of Metazoa and Metaphyta; but in the latter cases certain conditions are imposed upon it, and these include not only the ordinary conditions of nourishment, and of surrounding circumstance, but, as a rule, the further condition of amphimixis.

The Appearance of Amphimixis in the Organic World.

If we are unable to discover any effect of amphimixis which can render its prevalence intelligible, nothing remains but to accept the rejuvenescence theory. For not only is amphimixis found throughout the whole organic world so far as we know it, but the entire form of the latter has been controlled in a most fundamental manner, and, without amphimixis, would have been utterly different.

It has been shown above that the occurrence of an ontogeny in the Metazoa essentially depends upon the necessity for amphimixis; since this presupposes the concentration of the collective hereditary tendencies of a species in the nucleus of a single cell. But this is not only true of all the varied kinds of direct ontogeny: the complex and changing forms of alternation of generation in animals and plants are also, mainly and in the most important respects, dependent on the necessity for making amphimixis possible. I say 'necessity,' because I hold that everything real is also necessary, and that this is true even of the things we generally call useful; for I believe that in nature the really useful—viz. that which is useful when considered in relation with the whole of its consequences and not by itself alone—is also invariably necessary. *The useful becomes necessary as soon as it is possible.* In this sense we may regard amphimixis as necessary because it obviously involves a deep and essential use.

Its unusually elastic powers of adaptation show how far it is from being necessary, viz. essential to life, in the usual sense of the word.

If amphimixis is truly rejuvenescence, i. e. the hindering of an

otherwise inevitable death, we ought to find it as a fundamental process, occurring without a single exception. It is hardly necessary to say that this is not the case. Least of all ought its appearance to depend obviously upon external conditions of life. But this is certainly the case; *the periodicity of its appearance can be proved to depend upon adaptation.*

In many thousands of species of the higher animals amphimixis invariably makes its appearance at the outset of every generation, for no egg can develope without fertilization. This is true of the whole Vertebrate sub-kingdom. Isolated exceptions to this general law suddenly begin to appear in the group of the Arthropods. Certain eggs, in which we should have thought fertilization would be the necessary preliminary to development, have gained the power of developing unaided,—viz. the power of producing males alone (bees), while the same eggs, if fertilized, would produce females. In plant-lice, on the other hand, females emerge from unfertilized ova, and not one generation only, but two, three, and even many, succeed each other before a sexual generation occurs and, with it, amphimixis. How far this latter is from being a process of multiplication, and how superficial is the connexion which usually obtains between amphimixis and multiplication, are shown in the bark-lice, e.g. *Phylloxera.* In these it has already been mentioned that the sexual generation consists of minute animals devoid of mouth and of the power of taking food. The female lays a single egg, so that, as in the primitive form of conjugation, the number of individuals is not increased by reproduction, but diminished by half. Nature could hardly express with greater clearness the stress which she lays on amphimixis; nor could she argue in a more convincing way that increase is distinct from amphimixis, and that the quickening of new germs need not be dependent upon the latter.

If amphimixis were a process of rejuvenescence we could hardly believe that its occurrence in the life of a species would be so excessively fluctuating,—sometimes taking place in each generation, sometimes recurring after a lapse of two, three, or even as many as ten generations, sometimes being absent for forty generations, as I have proved to be the case in *Cypris reptans.* It might be suggested that the recurrence of amphimixis does not depend on the number of generations of

individuals, but on the number of cell-generations, and that continuous life is rendered possible by the reappearance of amphimixis after each million or hundred thousand generations of cells. We might also—as I have already mentioned—compare the 'agamic' cell-generations of Infusoria, which follow each other between two periods of conjugation, with the collection of cells composing the person of a Metazoon, and regard the ontogenetic cell-series, as a whole, as the equivalent of the millions of individuals which make up an Infusorian colony. In both these cases the rejuvenating and quickening influence of amphimixis may be supposed to endure for a certain number of cell-generations. I must admit that I consider such reasoning to be bad 'philosophy of nature,' i.e. playing with words which convey no distinct meaning. It is contradicted by the fact that the cell-cycle of ontogeny in the lowest representative of the Vertebrata, the Amphioxus, cannot be compared as to length with that of the higher members of the group; it is equally disproved by the phenomena of cyclical development, showing that in one case the effects of fertilization may extend through one ontogeny, in another through two, three, six, or even ten ontogenies, not to mention the case in which forty generations have elapsed without the occurrence of amphimixis.

If we regard amphimixis as an adaptation of the highest importance, the phenomena can be explained in a simple way. I only assume that amphimixis is of advantage in the phyletic development of life, and furthermore that it is beneficial in maintaining the level of adaptation, which has been once attained, in every single organism; for this is as dependent upon the continuous activity of natural selection as the coining of new species. According to the frequency with which amphimixis recurs in the life of a species, is the efficiency with which the species is maintained; since so much the more easily will it adapt itself to new conditions of life, and thus become modified.

Amphimixis must first have appeared among unicellular organisms in the form in which we now find it in most Protozoa (Flagellata, Sporozoa, Rhizopoda)—namely, as the complete fusion of two entire animals[1].

[1] Maupas (op. cit. p. 492) attributes to me the view that conjugation bears a different significance in the lower Protozoa from that which it possesses in the higher, and he describes this 'manière de voir' as

Since this process is in direct antagonism to reproduction, i.e. increase, it can only be repeated after long intervals, lest it should prevent the sufficient increase of a colony of such animals. Hence we find that conjugation recurs periodically among the Protozoa; and indeed--as Maupas has taught us in the Infusoria—only repeats itself after a great many (120-300) generations.

Amphimixis, as we have seen, only became possible among Metazoa by concentrating or packing all the predispositions into the restricted area supplied by the nuclear substance of a single cell,—and this must happen even when the adult body is composed of millions of cells, differentiated in the most diverse directions, and combined to form tissues, organs, and systems. The result of this arrangement is seen in a highly complex ontogeny; and it is obvious that many conditions of life may arise which render it advantageous that the increase of the species should not proceed exclusively by this long and intricate, and therefore dangerous road, and that accordingly the origin of each new individual should not be necessarily bound up with amphimixis. In this way we are able to understand the wide distribution and diverse forms of asexual reproduction among the lower Metazoa and in plants.

There is, however, another factor,—the appearance, in the two last-mentioned groups, of that complex form of individuality known as the stock. This is brought about by the budding or division of the person, a form of increase which renders possible a continuity of the persons proceeding from one another. Such increase is not associated with amphimixis, because the indis-

'superficielle,' etc. I have never held such a view; the only passage in my writings which can have given rise to such a misapprehension deals with the phyletic origin of conjugation ('Bedeutung der sexuellen Fortpflanzung, p. 52, translated in vol. i, see pp. 293-294). Anyone who refers to this passage will find a hypothesis, expressed with all reserve, suggesting the original significance of the fusion of two unicellular organisms. Conjugation must have had some beginning, and although I believe that in its present form it signifies a source of variability, it must originally have had some other meaning, for two Monera would scarcely coalesce in order to ensure variability in their descendants. A change of function must have taken place, or, as Dohrn has very clearly expressed it, a secondary effect associated with the original main effect has, at a later date, usurped the place of the latter. Maupas accepts conjugation in the form in which it exists, and makes no attempt to understand how it originated. I do not blame him for this, but is it really so superficial to investigate the origin of any phenomenon?

pensable mechanical conditions are wanting. Hence, in the formation of stocks, amphimixis does not appear in every generation of persons, but only periodically in certain generations, and from this follows an alternation between two methods of increase, viz. with and without amphimixis, or, as it is called, an alternation of generation. Many principles come into action in this mode of development, which we cannot stop to consider, above all the gradual development of high individualisation in the stock, through the differentiation of its persons on the principle of division of labour, as was expounded many years ago, in a most convincing manner, by Rudolph Leuckart.

We can furthermore understand why a longer or shorter series of generations elapses before amphimixis becomes associated with increase: a long interval is the necessary consequence of the formation of highly differentiated animal stocks.

I need hardly say that I do not, by any means, intend to imply that no change in the method of reproduction can have arisen without stock-formation. In the groups of polypes and medusae, among which the above-mentioned alternation of generation is so widely spread, we find species which do not form stocks, and which, after passing through a series of generations by fission or budding, return to the method of sexual reproduction. It is clear that in such cases, the omission of a detailed and dangerous embryogeny, together with the more rapid multiplication which accompanies the omission, has been the efficient cause which has limited amphimixis to certain generations. The fresh-water polype, Hydra, is an example of this. The duration of the 'agamic' period is so regulated by the external conditions of life that the concentration of the collective predispositions of the species in a single cell, which is associated with amphimixis, is at the same time made use of to form a resting-egg, which carries the species over the unfavourable seasons.

The adoption of entirely different methods by closely allied animals shows how little the existence and duration of the periods of asexual reproduction have to do with the number of cells composing a single individual. In one and the same group of Hydromedusae we find species with long periods of asexual reproduction side by side with others in which it has entirely disappeared, so that every generation proceeds from fertilized

eggs, and is therefore under the direct influence of amphimixis. It is well known that some Medusae are budded off from a polype-stock, and constitute the sexual generation of the latter, marking the end of a series of asexual generations; while other Medusae invariably arise from fertilized ova, and always produce eggs requiring fertilization, or, in other words, adapted for amphimixis.

The degree of organisation is, in yet another way, associated with the alternation of asexual with sexual generations, and thus with the periodicity of amphimixis. This new relationship between organisation and the recurrence of amphimixis, depends upon the fact that the asexual methods of reproduction by fission or budding are not possible in the highest and most complex Metazoa. They are only found in the lower groups of Metazoa, —the Coelenterates, Worms, and Echinoderms; disappearing in the Arthropods, Molluscs, and Vertebrates.

In these latter, we might well suppose that every act of increase would be connected with amphimixis; for,—since the structural complexity of the animals in question has rendered fission and budding impracticable and has therefore compelled a reversion to the unicellular germ and the occurrence of a detailed ontogeny in every generation,—it might seem probable that nature would not lose the advantage of connecting amphimixis with such a method of reproduction. We might therefore expect to find no exception to the occurrence of sexual reproduction in these groups. In this anticipation we should be deceived, inasmuch as it only appears in the great majority of cases. In the minority, amphimixis is very far from universal, in spite of a development from unicellular germs which would so easily have permitted it: furthermore, in this minority it was formerly connected with reproduction, and has been abandoned in different degrees. These cases of development from parthenogenetic eggs are, above all others, fitted to prove the importance of the principle of utility. The transformation of female sexual cells, at first directly adapted for amphimixis, into germs no longer requiring fertilization, is an artifice by which nature has contrived to avoid amphimixis when a high degree of structural complexity has prevented reproduction by fission and budding.

It may be remarked here that this suggestion supplies the answer to a difficulty which I was, for a long time, unable to

solve—namely, *the remarkable limitation of parthenogenesis to a few definite groups.* It is only found in Crustacea, Insecta, and Rotifers, and not among Vermes, Coelenterates, and Echinoderms[1]: furthermore, it does not exist in the two higher groups of Molluscs and Vertebrates. The solution to the problem is found in the suggestion that the lower groups of animals dispense with parthenogenesis, because it is unnecessary to them. Whenever increase without amphimixis became advantageous, it was more readily and better supplied by fission and budding. The absence of parthenogenesis in the higher groups of animals may probably be explained on the supposition that no force has appeared which would render it advantageous for amphimixis to be separated from the existing method of increase. This is especially clear when we investigate the grounds on which it must have become advantageous among the Arthropods.

The periodical occurrence of unfavourable conditions of life has often been suggested as the cause of the appearance of parthenogenesis in Arthropods and Rotifers. I need only refer to my already quoted work on *Daphnidae*, in which this question is considered at length. Whenever a species lives scattered over a small area subject to rapidly changing external conditions which are, for a short time, favourable to life and multiplication, and then suddenly become unfavourable or even destructive,—it must be a great advantage for the increase of individuals to take place with the greatest possible rapidity during the favourable periods. As indicated in my former work, the advantage of parthenogenesis in such cases lies in the fact that multiplication must become many times more effective when every individual is a female, or, to express the thought in more general terms, when every single germ-cell can produce a new animal. A further acceleration ensues from the omission of that retardation of development which is implied by the occurrence of copulation and fertilization.

From this point of view we can not only explain the appearance of parthenogenesis in general, but also its special form in

[1] I am aware that it is believed to occur in some Coelenterates, but it seems to me doubtful whether any true parthenogenesis takes place. And, in any case, isolated exceptions do not invalidate the significance of the rule.

particular cases. In those Daphnids which, like the species of *Moina*, inhabit small rapidly filled, but also rapidly drying pools, the number of purely parthenogenetic generations which succeed one another after the foundation of the colony, is small. In *Moina paradoxa* and *M. rectirostris* males appear in the second generation, and some of the females produce resting-eggs which require fertilization. If this did not occur, if sexual reproduction, viz. multiplication associated with amphimixis, did not take place very soon after the foundation of the colony, it would frequently happen that the latter would be destroyed by sudden drought, without the formation of resting-eggs to carry life in a latent condition over an unfavourable period, and the colony would simply perish. It may be urged that parthenogenetic eggs might have been provided with resting shells like those which are, as a matter of fact, found in other Phyllopods, for example *Apus*. But clearly the object is to confer upon the species the advantage of periodically repeated amphimixis, and this is therefore connected with the formation of resting-eggs, and reproduction is so regulated that the number of parthenogenetic generations is determined by the average duration of the favourable periods of life. Thus, among the marsh-dwelling Daphnids numerous purely parthenogenetic generations succeed each other before a sexual generation appears, while in those which inhabit lakes and are subject to uniform conditions of life interrupted only by the cold of winter, the cycle is still longer. In some species amphimixis may be entirely abandoned, and this seems to occur most readily in those which produce but one kind of egg, which must naturally be provided with a protective resting shell, rather than in those forming two kinds of eggs, of which only one is a resting-egg and requires fertilization. Thus it is well known that most of the colonies of the common *Apus cancriformis* are purely parthenogenetic, and the same is true of the greater number of fresh-water Ostracodes.

Ten years ago, when I first directed my attention to the parthenogenesis of these minute Crustacea[1], I was able to distinguish three stages of reproduction,—the first was found in

[1] Zoologischer Anzeiger, 1880, p. 72. 'Parthenogenese bei Ostracoden.'

such species as *Cyprois monacha*, of which every generation reproduces sexually; the second was found in those species in which numerous parthenogenetic generations alternate with a sexual one; and finally the third included species in which males have not yet been found: in one such species (*Cypris reptans*), forty consecutive purely parthenogenetic generations have been observed.

We cannot yet decide why the advantages of amphimixis have been entirely given up in this and other cases. We cannot at present solve, or even profitably discuss, every biological problem. But it is probable that we are dealing not with adaptation alone, but perhaps with a suppression of amphimixis by means of parthenogenesis. Everything which is desirable is not possible; and after parthenogenesis has once been incorporated in the hereditary tendencies of a species, circumstances may arise in consequence of which it may be transferred, by the power of heredity, to the remaining sexual generations also, without the possibility of any interference on the part of natural selection. Whether this explanation is in the right direction or not, it is at any rate clear, as regards the question under discussion (viz. the true significance of amphimixis), that the loss of an *advantage* may be intelligible in many ways, while the loss of a *process of vital rejuvenescence* must stand in direct opposition to the continuance of life.

It would be of the highest interest to consider more closely the various cases of parthenogenesis, from this point of view: we do not, however, possess sufficiently accurate knowledge of the vital relations of the animals in question to enable us to estimate the advantages conferred by the disappearance of amphimixis, or rather the introduction of parthenogenesis, in a larger or smaller number of generations. I may, nevertheless, be permitted to afford some indication of the line of argument.

Parthenogenesis plays an important part in the group of plant-lice and bark-lice, containing very numerous species. The ova may be deposited or may undergo embryonic development within the body of the mother. In either case the advantage of parthenogenesis depends, as in the Daphnids, on the extraordinary rate of multiplication, which naturally reaches the highest point in the viviparous *Aphidae*, because the offspring

actually produce embryoes within their own bodies before they are born. But here we have to do, not so much with the sudden termination of a limited and changeful developmental period, as with the greatest possible use of the opportunities afforded by an extremely rich nutriment of vegetable juices. The excessively rapid multiplication ensures the colony, and therefore the species, from destruction at the hands of its numerous foes, which, just on account of the abundance of food provided by the vast increase of their prey, become themselves still more numerous, so that the multiplication of these plant parasites must be carried on at the highest possible rate. Hence we find that many purely parthenogenetic generations succeed each other, while amphimixis is ensured by a single generation of males and females, appearing towards the close of the period in which the richest nutriment is supplied.

On the other hand, we find that in many *Cynipidae* a parthenogenetic alternates with a sexual generation, and it generally happens that the latter appears in the summer, and the former in spring or even winter. The often considerable structural divergence between these two generations depends upon the very divergent conditions of life to which they are respectively exposed, and above all upon the fact that the eggs are laid in various, differently formed parts of plants, necessitating therefore a corresponding difference in the ovipositing apparatus. But such considerations need not detain us here. The benefits conferred by the absence of amphimixis from the winter generation appear to me to follow from the exceptionally unfavourable conditions of life by which it is beset. Many of these small Hymenoptera, e. g. *Biorhiza aptera*, emerge in the very middle of winter, on warm days in December or January, and creep upon the oak-trees, laying their eggs in the heart of the winter buds, having laboriously bored through the hard protective scales with the ovipositor. Without taking food, and frequently interrupted by cold and the long nights, they carry on this work until all their eggs are safely deposited or until death from snow or cold puts an end to their labours. It is clear that such hard conditions must prove fatal to many of these insects before they have fulfilled their task, and it must conduce greatly towards the maintenance of the species, not only for all the time occupied in selection by the sexes and in fertilization

to be saved, but also for every survivor in the struggle to be capable of laying eggs with the power of developing unaided, in other words for every such animal to be a female.

Much might still be said as to the causes of the omission of amphimixis from one or more generations, but a few words will suffice to show that the appearance of parthenogenesis depends upon adaptation to the conditions of life,—*that reproduction without amphimixis has invariably originated from sexual reproduction, whenever it was required in order to gain some distinct advantage in the effort to maintain the species.* We may well assume that the advantages which the appearance of parthenogenesis must confer, outweigh the disadvantages involved in the giving up of amphimixis. Our estimate as to the effects of the latter is far less certain and precise than of the former. If, however, I am not mistaken in my views on the significance of amphimixis as the source of individual variation, it follows that its omission from a single generation or even from a series of generations may be easily compensated; for it always reappears, and mingles afresh the complex individual predispositions into new combinations. The injury caused by its withdrawal would be less as the fertility of the species was greater; with this is connected the fact that *parthenogenesis is chiefly found in very prolific species.* Those individuals which sink below the level of organization characteristic of the species could the more easily be eliminated in the struggle for existence without in any way endangering the life of the species. Perhaps this explains why, in some few species of Crustacea (*Cypris*) and of Insecta (*Rhodites rosae*), amphimixis has utterly vanished without having caused, up to the present time, any trace of degeneration in the species.

We may safely assume that the entire absence of amphimixis is to be primarily explained as an adaptation, and that the alternation between sexual and asexual multiplication met with in Hydromedusae, Cestoda, &c., has arisen from the demands made by the conditions of life,—demands similar to those which have determined the alternation between monosexual and bisexual generations found in Insecta, Crustacea, &c. In both classes of cases amphimixis has been restricted to certain generations because it was not necessary in all of them, and because such restriction was a great advantage.

The means by which this limitation is exercised are different in the two classes, not by any means because parthenogenesis could not have been introduced among the lower Metazoa, but because nature did not require it, but resorted to the far more practicable and flexible methods of fission and budding. When these ceased to be available, she was compelled to alter the sexual cells in such a way that their powers of development were no longer connected with amphimixis.

There are indeed no plants wholly devoid of the power of reproduction by buds. Not only the formation of stocks but also the copious increase of persons and stocks[1] by means of buds is everywhere at the disposal of nature, and she has made a lavish use of them. With this is probably connected the fact that parthenogenesis is unusually rare in plants and only occurs in a few groups. I must leave it to abler botanists to investigate the grounds upon which unicellular germs, originally adapted for amphimixis, have been, in certain exceptional cases, afterwards transformed into parthenogenetic germs. The alternation of generation, so prevalent among the lower classes of plants, takes a form somewhat different from that found in the lower groups of animals, inasmuch as, not only the multiplication which is associated with amphimixis, but also that which is without, viz. agamic, depends upon unicellular germs. Ferns, Mosses, and Lycopodiums produce vast quantities of spores, the unicellular nature of which certainly does not follow from any former connexion with amphimixis in remote ancestors. It is far more probable that the unicellular condition has proved necessary in order to confer other advantages which, as has been suggested above, depend upon a minute size:—the lightness which facilitates transport by wind and water, and the possibility of production in enormous numbers.

In conclusion, it has been shown that amphimixis is everywhere present among the vital phenomena of a species when its existence is without injury to other vital interests,—that it appears, in the Protozoa, independently of reproduction, when a connexion with the latter was possible but unnecessary,—and that, in the Metazoa, it is bound up with reproduction, inasmuch as its existence only thus became possible. It has

[1] For a definition of this term see page 213.

further been shown that its occurrence in the life of a species becomes more frequent according as its admission by the vital conditions does not entail other disadvantages. When neither the formation of stocks nor the most rapid multiplication of individuals in the shortest time is required, we find amphimixis connected with the origin of every new individual ; but whenever the existence of the species would be endangered if new generations could not arise from the old in the most rapid succession and without any interval, we find that amphimixis is not inseparably associated with every act of reproduction, but makes its appearance only in certain generations. All this clearly points to the conclusion that amphimixis is no indispensable vital condition, no renewal of life or 'rejuvenescence,' but a process which has indeed a deep significance, although it is not inseparable from the continuance of vital processes. This conclusion becomes even more evident when we recognize how precisely, in the alternation of agamic and sexual reproduction, the number of agamic generations is regulated so as to correspond with the conditions of the species. *The rare or frequent repetition of amphimixis in the life-history of a species is not determined by its physical nature but by the conditions of life.* Its regulation depends upon adaptation ; it may be entirely excluded and the life of the species still continues. I do not know of any facts which lead us, after recognizing all this, to assume that amphimixis is anything more than an essential advantage in the maintenance and modification of species.

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